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HOMOIOTHERMISM

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The Origin of Warm-Blooded Vertebrates

BY

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TO

GEORGE HOWARD PARKER

PREFACE

Many of the problems of biology result from the fact that changeful organisms live in changeful environments. Life always involves continual adjustments to environment. Animals which invade new types of habitats must be able to change their inherited adjustment patterns or they must possess inherent qualities which make them more or less immune to the effects of environmental changes.

The animals which dominate the earth today originated in the stable, saline, food-laden ocean. Primitive animals for the most part remained in the sea, but as the ages went by several types migrated into fresh water and a few of the more progressive types even took up life on land. Migrants into fresh water and land habitats left the stability of the old marine haunts of life, where they lived in a medium which resembled the fluids such as are found in all protoplasms, where there was no dearth of oxygen and very little change in temperature. In fresh water they received little compensation, for they were obliged to live where there was often great variation in salinity, oxygen, and temperature. But those that attained to the land, although they were obliged to endure extreme variations in temperature, had to secure all their body salts from their food, and were in continual danger of death from desiccation, were also able to live in a rarer medium which permitted rapid locomotion and by supplying an abundance of oxygen made rapid metabolism possible.

This book attempts to discuss the physiological and ecological aspects of one type of adjustment which has made successful life on land possible and has reached its climax in the attainment of thermal and chemical stability within the bodies of animals.

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HOMOIOTHERMISM

CHAPTER I

INTRODUCTION

Warm-blooded, or homoiothermic, animals unquestionably had their origin through evolutionary changes from cold-blooded, or poikilothermic, animals. By acquiring the ability to maintain a comparatively constant and high temperature, the former have become more or less independent of temperature changes in the environment. A homoiothermic animal lives at approximately the same rate at all seasons and at all latitudes, but a poikilothermic animal must slow down its life processes whenever its surroundings become cooler.

Of course warmth is not the cause of metabolism, but is one of the conditions for it. Homoiotherms have gained to some degree the ability to ignore the environment. They have done this by means of certain mechanisms for heat production, insulation on the outsides of their bodies, the transfer of liquids from certain parts of their bodies to others, and other adaptations. The cells within their bodies live at rather constant temperatures which are close to the optimum for metabolic activities. Some poikilotherms which inhabit cold oceans pass their whole lives below 0 deg. C. These animals must live on a lower metabolic and psychic level than such active cold water animals as penguins or whales. On

the other hand there are in parts of the tropics and in warm springs certain animals which inhabit an environment that never falls below about 27 deg. C. Lusk (1917) suggests that homoiotherms probably had their origin along the shores of tropical oceans, where they lived in an environment which continually had a rather high temperature to which they gradually became adjusted.

Metabolism requires a continual supply of energy and under usual conditions homoiotherms need more energy from day to day than poikilotherms. However, the change from the poikilothermic to the homoiothermic condition has not been related directly to a higher energy requirement, but to the use of new mechanisms for temperature regulation and better insulation. The protoplasm of the two types of animals is similar in its energy requirements, but poikilotherms are able to live at slower rates at lower temperatures, and homoiotherms, with the exception of certain hibernators which become quite inactive, are not. The homoiotherms have gained a great advantage in that they are able to live to practically their full capacity at all times, but they have also been obliged to assume certain limitations in order to attain this end. Their method of living requires the continual expenditure of a considerable amount of energy and the control of their metabolic processes has to some degree passed under the domination of various controlling mechanisms. If there is lack of correlation between these controlling mechanisms, the result may be death. The mechanisms for heat production must operate under rather accurate control and must be correlated with mechanisms for heat dissipation. If the former run ahead of or behind the latter, fever or subnormal temperatures result.

Homoiothermic animals have become adjusted more and more to uniformity in the conditions for metabolism.

They are now specialized for a peculiar mode of life, a life characterized by many mechanisms for maintaining uniformity in temperature, metabolic rate, salt and organic content of the blood, and reaction of body fluids. This specialization has been associated with the migration of vertebrates from marine and fresh water habitats to land. Animals which live in the ocean are surrounded by a medium which is quite constant in its composition and resembles the blood of vertebrates in its salt content. This medium in any particular locality does not vary rapidly or extremely in temperature or in its content of dissolved gases. Freshwater animals live in habitats which are often limited in extent and vary widely in temperature and in content of dissolved substances. Land animals inhabit a medium which is very constant in composition and is rich in oxygen, but varies extremely in temperature. They are in continual danger of desiccation and therefore require a continual supply of water.

The homoiothermic condition is an adaptation for living a life under constant conditions in a highly variable environment. It has enabled birds and mammals to become dominant in the land habitats on the earth. Some homoiotherms, like the whales and sea birds, have been able to return to the home of their remote ancestors and have again attained a considerable degree of success in the ocean.

This book is concerned with the physiological and ecological aspects of the evolution of poikilothermic into homoiothermic animals. In it we attempt to discuss evidence for the origin of homoiotherms, temperature regulation, the factors influencing rate of metabolism and growth, and other matters which relate to the adjustments associated with evolution from erratic, more or less intermittent, living to uniform, constant living.

CHAPTER II

THE TEMPERATURE OF THE EARTH IN TIME AND SPACE

The formation of the earth's surface was probably a prelude to the origin of primitive life. The temperature of the earth and its atmosphere has furnished the background which makes the interpretation of heat phenomena in animals intelligible. It has also, we believe, furnished the stage setting in the story of how some organisms have become homoiothermal.

The Primitive Earth.—The history of the earth is read in rocks and more recent events are more clearly recorded than those which were more remote. The late history is revealed with great fidelity but the earlier history is indistinct and, if traced back toward its beginnings, the indistinctness merges into obscurity. Thus the picture of the primitive earth is more a matter of inference than knowledge.

There have been many attempts to explain the origin of our planet. Astronomers and geologists now generally agree that the solar system was evolved in some way from a nebula of one form or another. The Planetesimal Hypothesis of Chamberlain (1916) perhaps has the most wide acceptance of any theory of earth origin at present. According to this hypothesis, the original nebula consisted of small bodies, molecules or aggregates, moving in orbits about a common center and forming a disk-like system. The bodies are assumed to have been controlled by revolution about the center of the nebula

and not by impact on one another, as the older hypothesis of Sir George Darwin required. Evolution appears to have consisted in the gathering of these small bodies, or planetesimals, into planets and satellites. The meetings and unions of planetesimals implied a relatively slow evolution of nebula into a solar system but the end result was inevitable. The planetesimal hypothesis therefore signifies a relatively slow growth of the earth.

What the temperature of the juvenile earth was is still a matter of speculation. The hypothesis of Chamberlain requires a much lower temperature than that of Laplace. Instead of consisting of a primitive molten globe the earth probably originated in a nebulous knot of solid matter on which fell scattered nebulous matter, and the latter probably did not have a high temperature. Liquefaction of the rocks only occurred locally as the result of heat generated by increased pressure and by radioactivity. This temperature problem thus becomes fundamental because, according to the opinion of Chamberlain, the earth may have had a temperature suitable to life long before it reached its present size—perhaps when it had attained to the magnitude of Mars.

The Primitive Atmosphere.—The primitive atmosphere was, by early geologists, held to be vast, hot, and heavy, containing all the water of the globe, all the carbon dioxide now in carbonated rocks, all the oxygen which has been added to the rocks by oxidation, as well as that portion of all these constituents which is now found in the atmosphere and in organic tissues. Such a condition was assumed because heat promotes the expulsion of gases from liquids or solids. The heat of the primitive earth was believed to have been sufficient to drive out all gases. As the earth cooled these gases were reabsorbed.

An atmosphere containing much carbon dioxide and water-vapor should give the earth a warm and equable climate. Such climates apparently did prevail at certain times during the earth's early history, and also at certain times later.

Temperature of the Modern Earth.—Organisms now live at a time when the earth has marked climatic differences, varying between the frigid polar climates and the tropical humid or dry conditions. The earth has been colder than it now is, and at times the climates of the past have been warm and fairly constant the world over. However, there probably have been, usually if not at all times, zonal belts and fluctuations in temperature. This is indicated by the types of ancient animals or plants, from which may be deduced and plotted the temperature curves of the past. Thus it is indicated that warm climates persisted during long geological ages and that the polar regions were then usually inhabited by plants and animals which were adjusted to winterless environments. Apparently temperature fluctuations were often greatest during the opening and closing of the periods and eras.

Very long, warm times were separated by shorter periods of cool to cold climates. Geologists have determined that there have been about seven periods of decided differences in temperature as indicated by the fossil remains in sedimentary rocks and by the characters of the rocks themselves:

1. Early Proterozoic
2. Late Proterozoic
3. Silurian
4. Permian
5. Triassic to Lias
6. Cretaceous to Eocene
7. Pleistocene

At the beginning and ending of the Proterozoic, Permian, and Pleistocene there were cold periods accom-

panied by extensive glaciation. Cooler climates have occurred when the land areas were largest, or most emergent, usually during the closing stages of periods or eras, and cold climates nearly always existed during or immediately following times of active mountain formation.

The two principal atmospheric factors in the regulation of climate are carbon dioxide and water-vapor. The latter is the more important of the two and is also the more variable. If both of these atmospheric constituents are present in great abundance, especially aqueous vapor, a thickened atmospheric blanket will be formed which will retard the heat loss of the earth and will also absorb a greater amount of the sun's radiation. When there is but little carbon dioxide gas and water-vapor, more heat is lost and less absorbed. Climates then become cooler and more variable. The amounts of carbon dioxide and water-vapor in atmosphere have varied much during the earth's history.

Sources of Heat.—There are two sources of the heat by means of which the earth surface may be warmed: (1) radiant energy and (2) the internal heat of the earth's mass. If either of these factors were to be removed, life could no longer exist on the surface of the earth.

Temperature of the Earth's Interior.—There are many reasons for believing that the interior of the earth is very hot. Volcanic phenomena, geysers, and hot springs show that the earth is very hot in certain localities, even near the surface. In going down into deep mines the temperature rises about one degree Fahrenheit for each 100 feet. While there is little probability that this rise in temperature which is usual near the surface would continue at greater depths, yet it indicates

that at a depth of a few hundred miles, temperatures may perhaps reach several thousand degrees. A slow dissemination of the internal heat toward the surface of the earth continually takes place.

Radiant Energy.—The chief source of radiant energy is the sun. The amount of energy received from the stars is not sufficient to produce a significant effect upon the earth, but that received from the sun is very great. It is measured by the heat produced when a given surface exposed at right angles to a beam entirely absorbs the radiant energy. The mean value of such determinations is called "the solar constant of radiation" and has been fixed by Abbot as 1.932 calories per square centimeter per minute. If this value were constant the earth would receive in a year something like one million million million million calories. This would be enough heat to melt a layer of ice 110 feet thick over the entire surface of the earth, provided there was no reflection.

The amount of radiant energy coming to the earth at any given point depends upon several factors, among which are longitude, distance between earth and sun, sunspots and other variations in the sun itself. The factor which influences the heat converted from solar radiation at any one point on the earth depends upon the intensity of the solar radiation striking a given area, and the absorbing capacity of the substance. A "perfect black body" is a highly efficient absorber of such radiations. Obviously, surfaces that reflect radiations well have little power to absorb. Snow is an excellent reflector and has much to do with low temperatures during winter months. Substances which are good transmitters of radiations likewise absorb little of the radiant energy coming to them. During volcanic eruptions the transmissibility of the atmosphere undergoes marked changes, with the con-

sequent diminution of temperature on the earth. Such changes occurred after both eruptions of Krakatau (1884–1886; 1903–1904).

The Capture of Solar Radiation.—The internal heat of the earth's mass and the heat converted from radiant energy are sufficient to create a favorable physical environment for life on the earth's surface. Life, however, could not have evolved to the complexity of organization manifested today in animals, and especially could not have climbed the phylogenetic tree to the branches occupied by the homoiothermic animals, save by the capture of sunlight.

In warming the earth's surface the energy of sunlight is converted directly from electronic energy to molecular energy. Living matter has found a way by which the energy of sunlight may be stored or conserved and translated into molecular energy at some future time when it will better serve the organism. Thus there seems to be a system of conservation of energy in living matter—almost a closed cycle of energy changes. The energy of sunlight is captured on one side of this cycle to compensate for the loss of energy on the other. This captured energy enters the prison gates of living substance through chlorophyll. It is transformed and mobilized to places where it awaits release. Thus living substance is not only a transformer of energy but an accumulator as well. Once energy has accumulated, plants and animals become reciprocating transformers of it, so that the energy wastes of one become the energy sources of the other. This matter will receive more detailed treatment in later chapters.

CHAPTER III

ANCESTRY OF HOMOIOTHERMIC ANIMALS

The general structure of the genealogical tree of vertebrates is now fairly well established. Since Cambrian times fishes gave rise to amphibians and amphibians to reptiles. From early reptiles came the birds and mammals.

Although some fishes, notably the tunnies (Boulenger, 1910), after activity may show a body temperature somewhat above that of the water in which they live, there are none which maintain a high and constant temperature comparable to that of birds and mammals and there is no evidence that any fishes have been able to do so in the past. Amphibians and reptiles, both aquatic and terrestrial, also may have body temperatures above the medium in which they live, but are not homoiothermic and apparently have never been so.

In speaking of the dinosaurs, Lull (1924) says: "That their activity, which implies increased metabolism, raised the bodily temperature during the time of such activity, it is, I think, safe to assume—an analogy is seen in the tuna among the bony fishes today—but that they possessed a mechanism for the maintenance of a constant bodily temperature irrespective of external conditions, as with birds and mammals, is sustained by no evidence thus far offered. In fact, their entire lack of heat-retaining clothing, such as the feathers of the bird or the hair of the mammal, negatives such a possibility." The same

appears to be true of the pterosaurs, or extinct flying reptiles.

Birds

Among several groups of ancient and modern reptiles the habit of standing more or less upright and walking, running, or leaping with the hind legs has been developed in various localities and at various periods. These bipedal reptiles are, and were, often quite agile. They commonly use their tails to help support or balance their bodies, develop processes on their pelvic bones for the attachment of muscles, and possess other characteristics adapted to their method of locomotion. Their fore legs are often small and delicate and serve more for balancing than support.

Heilmann (1926) has given a very careful account of the evolution of birds from reptilian ancestors. He believes that birds sprang from the Pseudoseuchia, a group in which the pubic bones already showed a tendency to extend backward. These reptiles were also related, though not directly, to the dinosaurs, pterosaurs, and crocodiles. The particular group from which birds arose were generally characterized by sharp-clawed first, second, and third fingers, and by a tendency to reduction of the fourth and fifth fingers; adaptations which indicate arboreal, climbing habits.

The evolution of birds apparently took the following course. Certain pseudoseuchians raised the forepart of the body off the ground and as they became bipedal the hind foot centered along the median line. From terrestrial runners or leapers these animals gradually changed to arboreal climbers. They leaped from branch to branch; long, parachute scales developed along the posterior borders of the fore limbs; these later became

frayed into feathers, which later spread over the whole body. In early stages of this evolution, the climbing fingers became elongated, and thus favored wing development. With the growth of wings a keel for muscular attachments projected more and more from the breast bone. The hind toe of birds undoubtedly originated in connection with adaptation to arboreal life. Heilman concludes:

> The accelerated metabolic process, finally, produced an increased caloricity, protected by feathering, until the warm-blooded state was attained. The air-sacs of the lungs have expanded, spreading through the whole body and filling the bones with air. The increase of all these activities, moreover, has also resulted in a considerable enlargement and a somewhat refining evolution of the brain.
>
> In this way the reptile, through millions of years and innumerable generations, has been changed into a bird.

Modern birds generally maintain a constant body temperature somewhat above that of mammals. This varies very little at different seasons of the year (Simpson, 1911) and is quite similar in primitive and specialized birds (Simpson, 1912). However, Stoner (1926) has recently reported that the temperature of the adult bank swallow, *Riparia riparia* (Linnaeus) may vary as much as 7 deg. C. and that of the young, 10 deg. C. Kendleigh and Baldwin (1928) made similar observations on house wrens. Atkins (1909a) observes that the osmotic pressure of a developing hen's egg rises from 5.5 to 7.3 atmospheres. The latter figure is about the same as that for bird's blood. "The view is put forward that birds are descended from organisms with an osmotic pressure of five atmospheres or less." The osmotic pressure of the internal fluids in the bodies of modern reptiles is about five atmospheres.

Mammals

There is a general agreement among vertebrate palaeontologists that mammals originated from the order of Triassic reptiles known as the Cynodontia. During Permian and Triassic times the cynodonts had developed temporal bony arches, a secondary palate, paired occipital condyles, heterodont dentition in which incisors, canines, premolars, and molars were differentiated, and a functionally important dentary. These reptiles developed a new type of jaw articulation, and the quadrate bone, which plays such an important rôle in lizards, became degenerate.

Hairs are believed to have been derived from reptilian scales and there is evidence which supports this view. The genital organs of primitive modern mammals, monotremes and marsupials, show transitional stages between those of reptiles and more specialized placentate mammals. The marsupium probably enabled early mammals to carry their eggs away from the nest. The eggs were thus better protected. Later the young mammal probably took the place of the egg in the pouch. Lactation probably came in with the acquirement of the homoiothermous condition. The oily fluid which perhaps at first served to lubricate the pouch and help keep the young warm later came to serve as a regular means for nourishment. The young at first licked milk from hairs; sucking succeeded licking and the young became in a sense external parasites on the mother. The placenta developed and the young were then able to obtain nourishment within the body of the mother and could thus grow to larger size before birth (Gregory, 1910).

In Cretaceous times the dinosaurs and other reptiles lost their dominant position among the animals of the

earth. Perhaps the mammals ate their eggs, perhaps they were unable to compete with the mammals on account of their lack of ability to endure cold, perhaps they passed away partly on account of their inferior locomotor mechanisms and brains, and because of wasteful methods of reproduction. At any rate, they were exterminated or greatly reduced in numbers and reptiles today hold a rather unimportant place. Representatives of very primitive Cretaceous mammals have recently been discovered in Mongolia (Gregory, 1927). These early insectivore-carnivore ancestors of modern mammals were already far from the beginnings of their careers; already differentiated into marsupials and placentals.

Among primitive, living mammals, the monotremes are probably not distinct from other Theria but are "the much specialized descendants of very early mammals" (Watson, 1916). They probably represent primitive ancestral conditions in their egg-laying habits, the arrangement of their genitalia in relation to a cloaca, and their somewhat variable body temperature. Among many types of placentals there are rather elaborate mechanisms for maintaining constant temperature, and these are not so well developed in more primitive mammals (Martin, 1903). Marsupials depend largely on evaporation through the lung membranes for the lowering of body temperature, and are the lowest animals to show heat polypnea. A rabbit also uses polypnea as a means of temperature regulation and depends largely on vasomotor regulation for the dissipation of heat; carnivores have somewhat more varied and effective mechanisms. Among homoiothermic animals there are various means and degrees of efficiency in the regulation of temperature.

Environment during Evolution of Homoiotherms

Vertebrates had their origin in the water and some of them have slowly spread into land habitats. The earliest vertebrates already had a long heritage from the past. Even their blood had a somewhat distant relation to sea water, which probably served their remote ancestors as a body fluid. Types which attained to life on land were obliged to develop resistance to loss of water and to endure great changes in temperature. One of the means of gaining relief from the continual and marked changes of land climates was the attainment of the homoiothermic condition. In other words, the ability to maintain a constant temperature which permits uninterrupted metabolic activity at approximately optimum rate is an adaptation to life on land, where climate is variable.

The earliest birds and mammals were carnivores and insectivores. Homoiotherms and seed plants evolved together and Berry (1920) believes that the evolution of the former was to be to a considerable degree dependent on that of the latter. The development of seeds and fruits furnished nourishment which was in concentrated form and which was available at all seasons of the changeful year. The land animals which took advantage of the newly developed seeds and fruits as food were thus relieved to a considerable degree of the necessity for continually seeking and capturing living prey. This surety of food supply made easier the maintenance of metabolism at a continuously high rate. "It may be suggested that the changing food supply which is due to the evolution of the flowering plants, and which is suggested as one of the important factors in the evolution of the higher mammals, was also one of the factors that

spelled the doom of the overgrown and specialized Reptilia of the Mesozoic." A giant dinosaur required tons of plant food, while a small mammal subsisting on seeds and fruits could remain active at all seasons. The development of seeds and fruits greatly increased the food resources of early mammals. Berry stresses the fact that differentiation among the flowering plants was soon followed by the great differentiation of mammals, beginning in the Eocene Period.

CHAPTER IV

RESPONSES OF POIKILOTHERMS TO VARIATIONS IN TEMPERATURE

It has long been recognized that, in so far as body temperature is concerned, animals may be divided into two large groups. These have been referred to as the cold-blooded and the warm-blooded animals. The first group includes animals, poikilotherms, in which body temperature changes with that of the environment; the second group includes those animals, homoiotherms, which maintain at all times a practically constant temperature which is inherently independent of the environment. In this chapter the responses of poikilotherms to heat and cold will be discussed.

Body Temperature of the Poikilotherms.—The lower vertebrates and all of the invertebrates belong in the group of variable temperature animals. Only the birds and mammals possess a means of regulating their body temperature which makes them independent of the temperature of the environment. How close the poikilotherms approximate the temperature of their environment cannot be stated with certainty. It will be seen from Table I that not all investigators agree. Many of the conflicting results reported as to the temperature of poikilotherms are likely due to the methods employed. By the use of precision instruments many of the variations may be eliminated and a better understanding of temperature relations now is being acquired.

TABLE I

BODY TEMPERATURE OF CERTAIN COLD BLOODED ANIMALS

(After Rogers, 1916)

Form	Range	Conditions and Method	Temperature of Animal above that of Environment	Observer
Medusa..........	....	....	0.27 deg. F.	Valentin
Earthworm.......	56 deg. F.	Several in glass by thermometer	2.0–2.5 deg. F.	Hunter
Leeches..........	56–54 deg. F.	Several in glass by thermometer	1.0–1.5 deg. F.	Hunter
Worms...........	....	....	4.4–5.8 deg. F.	Davy
Ceylon jungle leech	....	....	Same as water or air	Davy
Echinoderms......	....	....	0.40 deg. F.	Valentin
Snails............	54 deg. F.	Several in glass by thermometer	1.25 deg. F.	Hunter
Snail.............	76.25 deg. F.	....	0.25 deg. F.	Davy
Oyster...........	82 deg.	....	Same as water	Davy
Crustacea........	72–80 deg. F.	....	1 deg. below to same as water	Davy
Insects...........	62–83 deg. F.	....	8 deg. below to 10.5 deg. F. above	Davy Davy
Bees.............	19.2 deg. C.	Individuals thermoelectric	0.18 deg. C.	Dutrochet
Bees.............	....	Hive	0.25 deg. C.	Dutrochet
Bees.............	....	....	0.55–10.5 deg. C.	
Bees.............	57–69 deg. F.	Thermoelectric	Same as air	Phillips & Demuth
Bees.............	Below 57 deg.	Thermoelectric	Form clusters and raise temperature	Phillips & Demuth
Fishes:				
Bonita.........	80.5–78 deg. F.	Heart muscle	1.5–5 deg. F.	Davy
Trout..........	86–40 deg. F.	....	28 deg. below to 2 deg. F. above	Davy
Eel............	51 deg. F.	....	Same as air	Davy
Fishes (?)......	....	....	0.55 deg. F.	Martin
Fishes (?)......	....	....	1.38 deg. F.	Kraft
Fishes (?)......	....	....	6.2–9.3 deg. F.	Broussouet
Fishes (?)......	....	....	1.2–6.2 deg. F.	Broussouet
Carp...........	....	....	3 deg. F.	Boniva
Carp...........	....	....	0.86 deg. F.	Deprets
Carp...........	66.5 deg. F	Stomach	1.9–3.5 deg. F.	Hunter
Mackerel.........	80.5 deg. F.	Stomach	8.5 deg. F.	Davy
Herring..........	4.6–6.04 deg. C.	....	0.0–1.2 deg. C.	Simpson
Amphibia........	58–86 deg. F.	Rectal temperature	3.0 deg. below to 8.5 deg. F. above	Davy
Frog.............	....	In air	Temperature less than air	Berthold
Frog.............	....	In water	Same as water	Berthold

The factors which influence the temperature of animals may be regarded as either *extrinsic* or *intrinsic*.

The intrinsic factors are those that lie within the organism and act to produce a temperature different from that of the environment. The extrinsic factors are those imposed on the organism from without. These will be discussed first. Heat may be gained or lost by (1) conduction and convection and by (2) radiation.

Conduction.—Conduction means the loss of heat from a body at a higher temperature to one at a lower temperature by passage from particle to particle. For example, if one end of a copper rod is placed into a dish of hot water, heat will pass into the rod and along it until the other end becomes hot. This is molecular transference of energy. The amount of heat gained or lost by a poikilothermal animal through conduction will depend upon several factors; the most important of these are the amount of surface exposed, temperature gradients, and atmospheric humidity. The amount of heat gained or lost will vary directly with the *area of* the surface exposed. Since the area of the surface of a body increases to the second power when the mass is increased to the third power, a larger animal will gain or lose heat more slowly than a smaller one. The gain and loss of heat also depend upon the *moistness* of the surface. Most of the poikilotherms live in the water and are little influenced by this factor, but amphibians and reptiles which live in the air of course show marked differences in this respect. Amphibia nearly always have moist skins whereas Reptilia have dry scaly skins. The latter therefore lose heat more slowly. The nature of the surface is likewise a factor in the gain and loss of heat. A layer of fat at or near the surface will considerably decrease the rate at which heat arrives at the surface from the interior. The low thermal conductivity of fat is thus an important factor in the retardation of heat

loss. The subcutaneous tissues often cause a temperature lag or thermal gradient, which in a large animal will be several degrees. This factor is of most importance in the homoiotherm but nevertheless must not be considered as a negligible factor in the poikilotherms.

The heat lost by a body in a unit of time is proportional to the difference between its temperature and that of the surrounding medium. A warm body loses heat and becomes colder, while the environment becomes warmer. This transference of heat goes on until the organism and the environment are at the same temperature. The time required for this equilibrium to become established depends mainly upon the gradient between the integument of the animal and the immediately surrounding medium. The circulation of the blood tends to make the gradient greater and consequently a living poikilotherm will come more quickly to the temperature of its surroundings than will a dead one. This we have shown to be true of a turtle immersed in a water bath of constant temperature. The temperature was taken by a thermocouple placed in the coelomic cavity very near the center of the body. The surrounding water was kept in rapid circulation and the turtle was held stationary. The turtle weighed 278 grams and at the beginning of the experiment was transferred from a water bath which was 10 deg. C. higher than the experimental bath. The absolute temperatures were read with a standard mercurial thermometer calibrated to one-hundredth of a degree centigrade. The temperature differences were determined with copper-constantan thermo-couples. After one determination was made of the rate of heat transference from the living turtle to the water bath, the experiment was repeated with the same turtle killed by ether anesthesia. The experiment was then reversed

with a turtle weighing 278 grams with heat absorbed first by a living turtle and then with the same turtle dead.

Figure 1 illustrates how blood circulation apparently influences the temperature gradient between the surface of an animal and the surrounding medium. It is also interesting to note that, in consequence of the influence

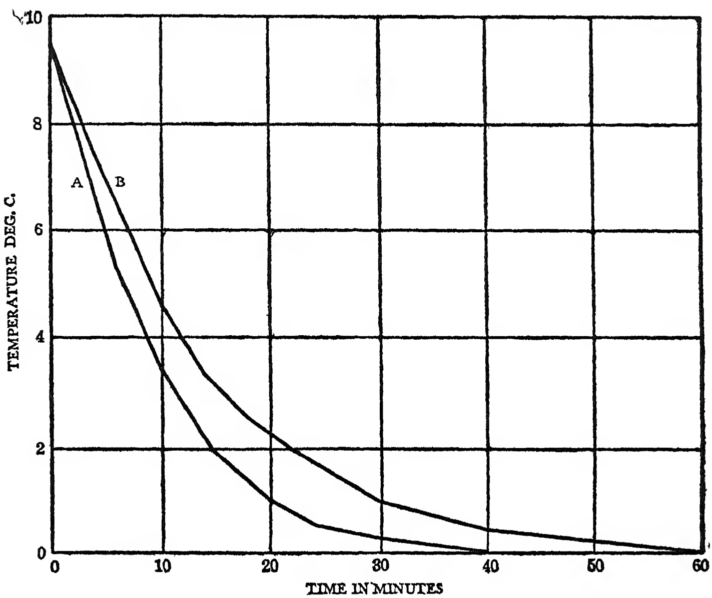

FIG. 1.—Rate of response to an altered environmental temperature in a living and dead turtle. *A*—living turtle; *B*—same turtle dead.

of temperature on the rate of heart beat and velocity of blood flow, the temperature of the turtle more quickly approaches the temperatures of the water bath at higher temperatures than at lower. If the medium is kept in motion the gradient will be higher than if it is stagnant. A terrestrial animal will gain or lose heat more rapidly if it is exposed to convectional cur-

rents or winds than if the air is quiet. In the absence of air currents a layer of air will form an envelope around the animal, decreasing the temperature gradient and preventing rapid conduction of heat. Humidity is obviously a factor only in the terrestrial animals. Water is a better conductor of heat than air. The more humid the atmosphere, the more rapid will be the gain and loss of heat if other factors do not change. The humidity of the atmosphere also influences the rate of evaporation of water from the surface of an animal's body. The maximum rate of evaporation will take place in an atmosphere containing no water vapor and the minimum in an atmosphere saturated with water vapor, assuming that temperature and other factors remain constant. Evaporation has a marked cooling effect on animals.

Radiation.—The transmission of heat by radiation is fundamentally different from that of conduction. Radiation implies vibratory movements of particles or electrons depending on their kinetic energy. If the temperature of the particles is increased, the velocity of the vibrations will increase. Conduction requires molecular continuity. In other words, one body must be in contact with another in order to have transmission of heat energy by conduction. One body may affect the thermal state of another body by radiation without being in contact with it, and also without affecting appreciably the intervening medium. Radiation is not dependent upon a continuous medium, such as air or water. In fact, it takes place quite readily in a vacuum.

The heat gained or lost by an animal through radiation depends on the area of its surface, color, and temperature. It has been proved experimentally that the absorptive and emissive powers of a body are equal. Therefore if the temperature of an animal is higher than

that of its environment it will radiate energy more than it absorbs from it, but if it be at a lower temperature, it will absorb more than it will radiate. The total emissive and absorptive power of a body is directly proportional to the area of the surface. A perfectly black body will absorb all radiant energy that falls on it; and, since a body cannot absorb more than is incident on it, the black body is considered as unity. There are no animals which have a skin that is perfectly black and consequently any animal can absorb only a part of the radiant energy incident. Likewise there are no perfectly white animals and therefore all must absorb some radiant energy. However, there are a few animals, such as the marine Coelenterata, which are such good transmitters of visible light that the radiant energy absorbed by them is negligible. Buxton (1923) gives an admirable account of the color of desert animals and emphasizes the importance of color as an adaptive feature to physical rather than organic environmental conditions. Desert reptiles with a scaly integument reflect most of the light that falls upon them and thereby resist to a large extent the radiant energy of the sunlight.

Pigmentation plays an important part in the gain and loss of heat in animals. For example a turtle, with its highly pigmented shell, may, when basking in the sun, have a body temperature higher than that of the atmosphere about it. The junior writer has performed an experiment which demonstrates this. A turtle was placed on a table in the laboratory beneath a source of radiant energy (an infra-red generator) and its resulting body temperatures are shown in Fig. 2. It will be observed that, while the atmosphere was not warmed appreciably, the temperature of the turtle rose constantly to a point higher than that at which a turtle could live. It appears,

therefore, that poikilotherms may have a higher body temperature than that of their immediate environment through the absorption of radiant energy. In a very warm environment highly pigmented animals commonly find long exposures to sunlight deleterious, and seek the shade or are nocturnal. In a colder environment pigmentation may be of considerable value because it would

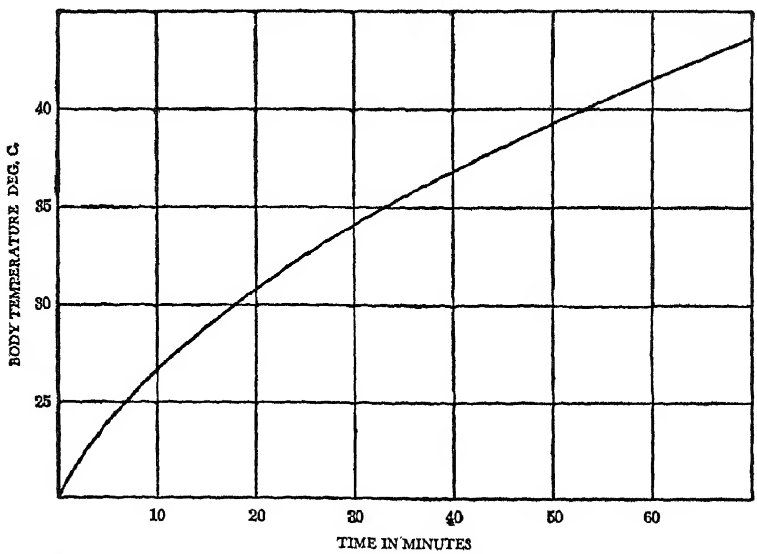

FIG. 2.—Rise in body temperature of a turtle when placed three feet away from a radiant source of energy. The circumjacent temperature remained unchanged.

aid in the absorption of heat. The temperature of a body is a determining factor in the amount of radiation from it. The total heat-loss by radiation is proportional to the difference between the fourth powers of the absolute temperatures of the body and its environment, if the area and nature of the surface remain constant. It follows then that a poikilotherm would lose little heat

by radiation if its own temperature differed little from the environment.

Poikilotherms respond to thermal alterations in the environment mainly in four ways: (1) torpidity, (2) migration, (3) acclimatization, and (4) tolerance.

Torpidity.—Metabolic processes vary with temperature, being slowed as an animal becomes colder and quickened when it is warmed. The limits at which an animal can carry on life processes lie between the freezing point of protoplasm and the coagulation of certain proteins by heat. As animals approach the limits of their toleration, certain of them may suspend their activities and go into a state of torpidity. Protozoa encyst; many insects become torpid during cold and dry weather; snails may seal up their shells; many fishes hibernate or aestivate during extreme climatic conditions; certain amphibians and reptiles hibernate during winter, but apparently do not hibernate if kept warm the year around.

Migration.—Many insects are known to migrate during changing climatic conditions. Fishes, such as herring and sardines, in summer live near the surface and store fat, but in winter descend to greater depths and lose fat. Marine fishes are sensitive to differences of 0.2 deg. C. Ward (1921) states that the migration of salmon is primarily controlled by temperature, the fishes choosing the cooler branches of the rivers as they move upstream. Amphibians such as Necturus move into the deeper and colder water during the summer months, and many frogs regularly alternate between aquatic and terrestrial habitats as the seasons change.

Acclimatization.—Dallinger (1880) showed that by raising the temperature of a culture of flagellates, he could raise their limits of tolerance from 23 deg. to

70 deg. C. Miss Behre (1918) has found that Planaria will quite readily change its limits of tolerance to high or to low temperatures. Acclimatization of vertebrates has been investigated by Davenport and Castle (1895). They tested toad tadpoles and found that the limit of toleration could be increased several degrees. Loeb and Wasteneys (1912), using Fundulus, demonstrated an increased resistance to heat and cold after continued exposures to extreme temperatures. Davenport (1897) suggested that increased tolerance to extreme temperature may result from lowering of the water content of protoplasm. Miss Behre believes that an adjustment of metabolic rate is an important factor in acclimatization. Hathaway (1928) has shown that continued exposures to high or low temperatures progressively raised or lowered the limits of tolerance of several species of fishes. He states also that fishes which inhabit shallow water (bass, bluegill, and sunfish) undergo a change of tolerance by acclimatization much more readily than the perch, which is typically an inhabitant of deep, cool water.

Tolerance.—Many animals are very susceptible to temperature changes and succumb if the thermal variation of their environment exceeds a few degrees; other animals resist or endure extreme temperature changes. Those in which the optimum range is narrow are said to be *stenothermal.* Those which endure the great variation in external temperature are *eurythermal.* Land animals as a rule are eurythermal to a greater degree than those in the water. In the latter group are such animals as the corals, which live largely in tropical seas. The carp and the goldfish are examples of freshwater forms which usually feed only between about 6 deg. and 30 deg. C. Eurythermal animals are illustrated by forms like the brine shrimp (*Artemia salina*). This crustacean

thrives in salt marshes and in pools which are opposed to the full radiating and evaporating power of the sun for the purpose of making salt. Centipedes are reported to range from hot plains and to the snow-covered peaks of mountains on the island of Cyprus. The common European eel is found from Ireland to the Nile. The American eel is found from the Caribbean to the Great Lakes. The water snake (*Tropidonotus natrix*) is found from Sweden to Algeria. Many other species of animals range through a variety of temperature conditions.

The extreme minimum temperatures which poikilothermal animals can tolerate are near the freezing point of water. Below this, metabolic activity ceases. Some marine animals in arctic seas live in water which is a degree or two below zero and are protected from freezing by the salts in their body fluids. Extremely low temperatures during a considerable part of the year do not prevent the successful existence of land animals if there is a warm season to allow for growth and reproduction.

The problem of toleration of high temperatures is unlike that of low temperatures for the reason that the effect of the former is principally chemical and usually involves a permanent change in the living protoplasm, while that of the latter is physical and produces a suspension of activities which are resumed with the return of favorable circumstances. The toleration of high temperatures is usually accomplished by means of alterations in the physico-chemical state of the protoplasm. Insects, for example, lose water in hot surroundings. Brues (1927) reports many insects living at 30 to 40 deg. C. in hot springs. He found "blood worms" developing at 50 deg. C. Snails, amphipods, and isopods were also observed living in similar conditions. Vertebrates were found to be rather uncommon, rarely survived in

water over 25 to 30 deg. C., and apparently never lived at temperatures of more than 40 deg. C. Tadpoles, however, were found living in water very near this limit.

It is a very interesting ecological point that nearly all groups of animals that are represented in freshwater contain a few species known to inhabit hot waters. The forms that adjust their tolerance to high temperatures are extremely varied.

Aquatic animals may have great difficulty living in warm water because of the small amount of dissolved oxygen. Many of the species which inhabit hot springs obtain their oxygen from the air. It is perhaps significant that the animals living in such situations where the essential elements, salts, oxygen, *p*H, etc., may be very unlike the ordinary freshwater conditions, show a greater resemblance to freshwater forms than do the marine forms which have always lived in the sea, where they are never obliged to resist great fluctuations in the temperature of their environment. Apparently animals which now live in waters which have high temperatures have been derived rather recently from typical freshwater animals and not from their more marine ancestors.

Body Temperature of Poikilotherms.—While it appears from the observations of many of the older observers that the body temperature of poikilotherms may differ as much as several degrees from that of the environment, later workers have found that such temperatures may resemble each other very closely, even to hundredths of a degree. Rogers (1927) found that the earthworm, salamander, clam, and goldfish in rapidly circulating water, had body temperatures of almost exactly the same temperature as the surrounding water. In the experiment summarized in Fig. 1 the body temperature of a turtle soon came to the same temperature as the

surrounding water bath. The same has been found to be true when salamanders and frogs are used. Thus it appears that with precise temperature measurements, little or no heat regulation obtains in the poikilotherm. Hence the temperature of the poikilo-organism is apparently determined through the gain and loss of heat controlled by aforementioned extrinsic factors.

CHAPTER V

RESPONSES OF HOMOIOTHERMS TO VARIATIONS IN TEMPERATURE

For every animal there is apparently an optimum range of body temperature within which life-processes are adjusted to proceed smoothly. This range is comparatively wide in the poikilotherms, but rather narrow in the homoiotherms. Since homoiotherms maintain an almost constant and optimum internal temperature, they are little affected by external temperature changes unless the alteration is great enough to overtax or break down their heat-regulating mechanisms. Thus it appears that all animals have an optimum range of external as well as of internal temperature. Poikilotherms have a relatively wider range of internal optimum temperature compared with the homoiotherm, but a relatively narrower range of external optimum temperature (Fig. 3).

The Body Temperature of Homoiotherms.—The average temperature of mammals is about 39 deg. C. That of man is about 37 deg. C. That of the duckbill (*Ornithorhynchus*) and spiny ant-eater (*Echidna*) is about 25 deg. C. and is much more variable than in other mammals. Birds have an average temperature about 5 deg. C. higher than the mammals.

The variation in the body temperature of the more primitive mammals is more approximately and imperfectly regulated in comparison with the higher mammals. There are few references to transitional stages between

the poikilotherms and the homoiotherms. Martin (1903) has discovered that certain of the primitive mammals of Australia have an imperfect means of heat regulation. He found the duckbill to be almost cold-blooded, and the Australian anteater showed a fluctuation of about 10 deg. C. in body temperature with a change of 30 deg. C. in the surroundings. The kangaroo and other marsupials exhibit a somewhat better control. The placental ani-

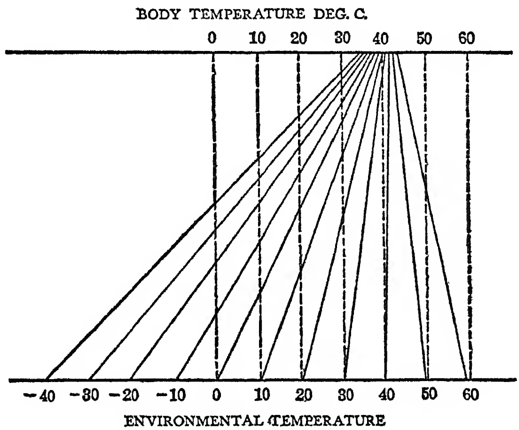

FIG. 3.—Difference between body temperature and environmental temperature in poikilotherms (– – – –) and homoiotherms (———).

mals have the most highly perfected regulatory mechanism. The sloth (*Bradypus cuculliger cuculliger* Wagler), one of very primitive placental forms, shows a rather imperfect mechanism of heat regulation. Kredel (1928) has shown that variation in the air temperature surrounding this animal will produce a relatively marked change in the body temperature.

Homoiothermal animals respond to environmental temperature variations by: (1) physiological regulation of gain or loss of body heat, (2) morphological adapta-

tions, (3) parental care of young, (4) migration, (5) hibernation, (6) storing of food, (7) occupation of homes which furnish more or less insulation, (8) the wearing of clothes.

Regulation of Body Temperature.—The regulation of body temperature will be discussed in Chapter VIII and hibernation in Chapter X. Many mammals protect their young from adverse temperature conditions. New-born rats and mice are unable for some days to resist changes in atmospheric temperature. The human infant must be protected for several weeks after birth and is easily chilled by exposure to cold. The young of the marsupials are carried in a pouch and are thus kept warm within the mother's body. Among many species of birds the young are kept warm by the heat from the mother for some time following hatching. Apparently the mechanism of temperature control is not completely functional at the time of birth, even in the higher mammals.

Migrations.—Many animals, notably the birds, migrate during certain seasons of the year and thus escape temperatures which might be deleterious. Migration, however, is apparently not always brought about directly by temperature variation and the advantage that may be derived by migration as a means of protection against extreme temperature changes is probably secondary to those associated with the securing of food and reproduction.

Morphological Adjustments.—Animals are provided with certain morphological adaptations for restraining the loss of heat through the skin. The more important are: (1) the subcutaneous adipose tissue and (2) the natural hairy or feathery coverings of the body. These vary greatly in different environments and with the degree of temperature fluctuations. The importance of the

subcutaneous fat is seen in the case of the homoiothermic marine animals in the Arctic. Such animals live habitually among the ice floes in a medium which conducts heat at least twenty times better than air and yet they are able to maintain a body temperature of between 35 and 40 deg. C. The outer layer of skin is subjected to conditions that would lead to an enormous loss of heat were it not for the layer of fat insulating the deeper tissues from the skin.

Insulation.—Homoiotherms living in the air are protected from heat loss by feathers and hair. These structures inclose a layer of air close to the body. By restricting the movement of this insulating air, much less heat is carried away from the body. Rubner (1903) determined the value of the hair of the guinea pig in saving heat. He found that normally the average loss of heat by radiation and conduction was 3.37 Cal. per hour. After the guinea pig was shorn the hourly loss was 4.19 Cal., *i.e.*, 33.3 per cent more. Hair or feathers have little value to animals living in water, for when the air spaces between these structures are filled with water heat is readily absorbed by the surroundings. Water birds obviate this difficulty by having oily feathers which do not readily become wet and these obstruct the passage of water to the air spaces next to the skin. They are often also well insulated with subcutaneous fat.

Resistance to Extreme Temperatures.—When a mammal loses heat to excess it is no longer able to maintain its temperature at a constant level. The lower the temperature of the body falls, the greater will be the disturbances thereby produced. The highest nerve centers are the first to suffer from such cooling. The medulla, where the important centers are located for the maintenance of various vital physiological processes, is not

affected until there is considerable reduction. Tigerstedt (1906) observed a man who retained consciousness with a temperature of only 26.7 deg. C. and discusses persons who recovered after extreme exposure during which the temperature of the body fell to 24 deg. C.

An increase of the temperature beyond certain limits involves general disturbances in the health of an organism. In general animals stand a decrease better than an increase in temperature. A rise of only 2 and 3 deg. C. may cause very severe disorders. A temperature of 41 or 42 deg. C. in the human body is regarded as a very dangerous symptom if prevailing for more than a short time.

Constancy of Body Temperature.—While a given individual is said to have a certain body temperature, it should not be assumed that the entire body is at the same temperature; in fact, such is not the case. The differences between various parts of the body may amount to several degrees. This has been notably demonstrated by Bazett (1927) and his co-workers. By means of specially designed thermocouples he has shown that temperature gradients exist in the body, the internal temperatures highest and decreasing toward the exterior. The gradient is greater when the temperature of the environment is lower.

Homes.—The usual functions of the homes built by animals are as refuges from enemies, often with particular reference to guarding and rearing the young, and as places for storing food. In many cases homes also serve for protection against the elements, a shelter against storms, and an inclosure for protection against the extreme temperature changes of the surroundings. Some animals build their homes of vegetation; others burrow beneath the ground beyond the frost line, where they may

hibernate. Man enjoys more advantages from his homes than any other animal and of course provides special means to prevent extreme changes in temperature.

Clothing.—Man alone among animals has become independent of temperature fluctuations by inventing clothes. In cool countries he endeavors to protect himself by keeping his skin covered. Only about 20 per cent of his skin is normally exposed to air. He varies the amount of surface exposed and the thickness of this artificial covering with the climatic changes. The air in and within clothes is a much poorer conductor of heat than the fibers from which fabrics are made and furnishes excellent insulation. This is especially true of that in the furs which man finds ready-made on the bodies of other mammals. The greater the thickness of clothing, the thicker is the layer of contained air and the greater is the prevention of heat loss from the body. Moisture absorbed by the clothes and filling up the air spaces decreases the effectiveness of the clothes. Savage races living in Tierra del Fuego in a cold moist climate usually do not wear clothes but a layer of oil over their bodies.

Temperature Regulation.—The mechanism of temperature regulation is not fully developed in many species of mammals until after birth. Some mammals, however, have the ability to maintain a very constant temperature from the first. For example this is true of the guinea pig, which has a well developed nervous system at birth. Other species, like the rat and the pigeon which are born helpless and require parental care for some time, do not come into possession of the power to regulate their loss and gain of heat for many days after birth. A newborn child is not able to control its bodily temperature well for several weeks. It is probable that this post-embryonic development of the regulatory mech-

anism is dependent upon the development of the neuromuscular apparatus which goes on at the same time. Kendeigh and Baldwin (1928) found that the resistance of young house wrens against cold follows the sigmoid growth curve. Such development of temperature resistance, according to these authors, is due largely (1) to the mass of body increasing faster proportionately than the external dissipating surface; (2) to the development of a feathery covering; (3) to the development of an internal dissipating surface, which probably is under nervous and respiratory control; and (4) to the production of heat by the metabolism. They believe the third factor is the most important.

CHAPTER VI

FACTORS INFLUENCING RATE OF METABOLISM

Metabolism is the chief source of the heat which maintains the constant temperature of homoiotherms. An animal may promote the retention of heat within its body by insulation or the transfer of body fluids and it may, if febrile, lose heat by surface conduction, radiation, or evaporation. The chief source of the energy which continually supplies animal heat is the oxidation of carbohydrates, fats, and proteins. If the surroundings of a homoiotherm become colder, its body usually responds by a greater degree of internal chemical change and energy is thus supplied to keep the body temperature constant.

The quality of metabolism is quite similar in poikilotherms and homoiotherms, but the quantity is strikingly different. The daily energy requirement of a fish is only 4 per cent of that of a mammal of the same weight. The life intensity, or rate of living, of a rabbit is 25 times that of a pike (Rubner, 1924). Because a homoiotherm lives at a more rapid rate, it must continually have more fuel for its metabolic processes and this is largely supplied in its food. A small animal requires porportionally more energy than a large animal of the same type because its surface permits more rapid dissipation of energy. On account of the comparatively slow rate of metabolism in poikilotherms such mass-surface relations

are correspondingly less important. A mouse requires much more food per gram of body weight than an elephant, but the differences between the food requirements of a little lizard and a giant crocodile are less significant.

As metabolism has been and is of prime importance in the origin and continuance of homoiotherms this chapter is devoted to a brief consideration of the factors which are chiefly concerned with its variations in rate. In this connection age, temperature, respiration, food, glands, desiccation, rhythms, and nervous control will be considered.

Age.—In all animals the rate of metabolism probably varies more or less at different ages. The fertilization of a sea urchin egg is soon followed by an increase in metabolic rate. As development proceeds the rate may increase or decrease. The development of a yolk-laden fish egg may proceed slowly until there are mechanisms for transporting food and then progress at a more rapid rate. When inert substances are being assimilated or when profound reorganizations are taking place in the bodies of animals, the metabolic rate may be slow. A Drosophila pupa shows a decrease in its metabolism during its second day of development, then the rate gradually increases up to the time of the emergence of the adult fly (Bodine and Orr, 1925). Various arthropods and chick embryos show differences in rate of heart beat and respiratory movements which are characteristic of particular ages (Crozier and Stier, 1927a; Henderson, 1927).

In youth a fish (Knauthe, 1898) or a mammal (Lusk, 1917) has a high rate of metabolism and this gradually grows slower, with some variations at such times as the annual spawning or the age of puberty. On the other hand the metabolic rate of amphibian tadpoles

which are undergoing metamorphosis progressively increases (Helff, 1923). Such changes in tadpoles are associated with profound bodily modifications. The stomach and intestine grow shorter through autotomy, autolysis, and phagocytosis; the food changes from vegetation to flesh. Of course other influences may be associated with age in affecting the rate of metabolism—men commonly have a higher rate than women; various species of salamanders appear to show characteristic and consistent differences (Helf, 1928).

Temperature.—In general poikilotherms live faster at higher temperatures and slower at lower temperatures, while homoiotherms live continually at approximately the same rate, but expend more energy at lower temperatures in order to furnish bodly heat. The metabolic rate of a fish, amphibian or reptile is rather closely associated with outside temperatures. The respiratory exchange, which is a reliable indicator of the rate of metabolism, in a turtle is approximately related directly to the temperature of the surrounding medium (Hall, 1924). Van't Hoff's Law for the velocity of chemical reactions in relation to temperature holds for the rate of heart beat of salamander embryos (Laurens, 1914). As the temperature of the water in which a fish lives rises, the amount of nitrogen excreted steadily increases (Knauthe, 1898). At temperatures below 6 to 9 deg. C. adult freshwater fishes cease to eat altogether, but young fishes continue to eat at lower temperatures than adults (Haussman, 1897; Knauthe, 1898; Pearse, 1919; Hathaway, 1927). However, there are species of fishes in some localities which pass entire life cycles at or near 0 deg. C., and others which never know temperatures below 45 deg. C. (Murray, 1914, 1914a). Particular species may have peculiarities or have become adjusted

to life at extreme temperatures, but in general the statement at the beginning of this paragraph is true.

At lower temperatures a poikilothermic animal often has a body temperature which is somewhat above that of the environment. The tunny may thus show a temperature more than 3 deg. C. above that of the surrounding water (Murray, 1914). In turtles, Baldwin (1925) found a non-critical range between 10 to 27 deg. C., where body temperatures were at times from 1.5 to 3 deg. C. above the surroundings, but at lower temperatures, and especially at about 4.5 deg. C., the body temperature showed a marked tendency to remain higher than the environment. He believes there is thus "a slight tendency to compensate for critical changes in the environment." McClendon (1918) and others who have studied the relations of temperature inside and outside various invertebrates and aquatic vertebrates find no such tendency. This is quite a contrast to conditions in the body of a mammal. A man, for example, has a high degree of ability to compensate for environmental changes in temperature. He maintains a constant temperature and gives off no more heat at 18 deg. C. in a room under a blanket than when in water having a temperature of 37 deg. C. (Benedict, 1914). In passing from fishes through the various classes of vertebrates to mammals and birds there is increasing control of rate metabolism and body temperature by nervous mechanisms. For example, the rate of respiration in a turtle is controlled largely by the temperature of the animal's neck. The temperature of the blood going to the head affects the respiratory centers in the brain. The temperature of the center cells is thus a more potent influence than the general activity or temperature of the body as a whole (Lumsden, 1924). In mammals the presence of carbon dioxide in the blood

passing to the respiratory centers influences the rate of breathing movements.

At high environmental temperatures, above about 37 to 40 deg. C., many homoiothermic and poikilothermic animals do not flourish (Rubner, 1924a). The reasons for this are not altogether clear, but they are, of course, quite different from those related to the slow metabolic rates which limit the activities of most poikilotherms at low temperatures.

Respiration.—There are two types of respiration: external, which is concerned with the bringing of oxygen into the body of an animal and with the elimination of waste gases; and internal, which supplies oxygen to tissue cells and permits such cells to eliminate their waste products. The oxygen consumed is perhaps the best index of the metabolic rate of an animal and is, of course, the chief agent, through oxidation, for producing animal heat and maintaining body temperature. Judged by oxygen consumed and carbon dioxide eliminated, there are considerable variations in the metabolism of individuals and of species. There are also many influences which temporarily affect respiratory movements and the exchange of gases for respiratory processes. The oxygen-carrying capacity of the blood of various marine fishes is apparently related to the degree of activity which each species normally shows. These fishes are each adapted to a certain metabolic level and the limiting factor to some degree is the rate at which oxygen can be supplied to the tissues. If two bullheads are put in an aquarium together they will show higher rates of exchange for respiratory gases than if they are left by themselves. The presence of one individual apparently influences the rate of respiration in the other. The oxygen consumption of different species of salamanders

differs characteristically and widely (Helff, 1928). Planarians, insects, and mammals after feeding show an increase in respiration which takes place before the food is being digested and appears to be due to increased activity of entoderm cells (Amberson, Mayerson, and Scott, 1924). When animals are desiccated carbon dioxide production increases rapidly when about half the vital limit is exceeded (Caldwell, 1925). In many invertebrates oxygen tension is related more or less directly to oxygen consumption, but this is not true of a vertebrate like Fundulus, which reaches a critical point and dies when the oxygen supply decreases. The metabolism of a fish cannot fall below a certain minimum limit (Amberson, Mayerson, and Scott, 1924). Some vertebrates, however, like turtles, which have a large storage capacity in their lungs, can get along for several hours at rather high temperatures without carrying on any external respiration (Lumsden, 1924).

Many factors influence respiratory processes directly or indirectly. Numerous invertebrates are able to reduce their respiration or cease to breathe altogether for long periods of time when oxygen is lacking in the environment (Pearse, 1926). More highly organized animals, in which more authority has been delegated to nervous control, cannot do this to such an extent and homoiotherms of course quickly suffocate if a considerable supply of oxygen is not continually available. Gesell (1926) has recently suggested that "changes in the hydrogen-ion concentration of the respiratory center rather than of the blood constitute the prime factor in respiratory control." He believes that oxygen supply controls the amount of lactic acid present and that the effects of this substance and carbon dioxide exert a combined influence indirectly when present in the blood and directly when

present in the respiratory center itself. In primitive protoplasm respiration is the direct result of and conditional for metabolism, but in more specialized animals there is much circumlocution in control. Individual idiosyncrasy, racial pecularity and physiological, environmental, psychological, and other factors may modify its rate or method.

Food.—Food supplies the fuel for metabolism. At low temperatures poikilotherms require little or no food, but homoiotherms under the same circumstances need an increased supply. However, an isolated heart of a poikilotherm requires two or three times as much sugar at low as at high temperatures. In a normal animal the sugar in the blood varies in accordance with such needs (Mansfield and Pap, 1920). This indicates that the tissue cells of poikilotherms, as well as those of homoiotherms, tend to oxidize more food at lower temperatures, but in the former the rate of metabolism is so much slower at lower temperatures that there is an actual decrease. Another characteristic of metabolic processes which intensifies this effect is the general tendency of animals to store fat during warm seasons and utilize this for metabolism during cooler parts of the year (Fage and Legendre, 1914; Pearse, 1924).

The amount of food required to carry on a particular amount of metabolism at a given temperature does not appear to differ markedly in poikilotherms and homoiotherms. The protoplasms in the two types of animals have similar needs. Page (1895) determined that a trout could subsist on food equal to about one per cent of its own body weight daily. Centrarchid and silurid fishes apparently need about six per cent (Pearse, 1924). The former eat about three times as much at 20 deg. C. as at 10 deg. C., and if kept at 10 deg. C. for several

weeks gradually eat less (Hathaway, 1927). A young smelt in May needs daily 1 mg. of food; in July, 2 mg.; and in September, 4 mg. A young herring in July requires 26.6 mg.; in September, 49.9 mg., and in October, 38.8 mg. (Pütter, 1909). Even with lower body temperatures the food requirements of poikilotherms are similar, in some cases at least, to those of homoiotherms. An average man requires organic food equal to only one to two per cent of the weight of his body each day.

Food is prepared for assimilation by digestion and its energy is released by the activity of catalytic agents. It has long been known that the digestive enzymes of homoiothermic animals have their optimum for activity at about 37 deg. C. and the recent work of Kenyon (1925) is of particular interest because it shows that the same is true for poikilothermic vertebrates. When reptiles gave rise to mammals and birds there were apparently no radical changes in the methods of digestion, assimilation, or energy release through metabolism.

The character of the food which any animal eats may have a profound influence on metabolism. It is well known that various foods have varying values as producers of energy. For example, Rubner's standard caloric, or heat producing, values are, in calories per gram of food; protein, 4.1; fat, 9.3; and carbohydrate, 4.1 (Lusk, 1917). Proteins, of course, have greater value as tissue builders than carbohydrates or fats but are more expensive as heat producers because more work is required to release their energy. Certain foods like vitamins, and certain protein compounds such as tryptophane, do not appear to have their chief value in the amount of energy or material they furnish, but in peculiar qualities which are as yet not wholly understood. There are also certain secretions like thyroidin and

pituitrin which exert a profound influence on metabolic activity and growth. There is at present no evidence that poikilotherms differ essentially in their digestive and assimilative processes from homoiotherms. They are susceptible to injury by lack of vitamins, monotonous diets, and other dietary deficiencies in the same way that homoiotherms are (Pearse, Lepkovsky, and Hintze, 1926). They are affected in much the same way by thyroid extracts and those of other ductless glands (Helff, 1923).

Starvation.—Among vertebrates there are many species of fishes, amphibians, reptiles and mammals which regularly pass long periods without food during aestivation or hibernation, and there are many which can endure long fasts. Both these types of quiescence are associated with changes in metabolic rate. An eel has been kept without food for 657 days. During this time the body cells decreased 10 per cent in size, but their number remained approximately unchanged (D'Ancona, 1928). Two species of centrarchid fishes were kept in filtered water at about 20 deg. C. for two months without food (Pearse, 1925). Turtles (*Chrysemys*) lived for nearly a year under the same conditions (Pearse, Lepkovsky, and Hintze, 1926). Some birds when starved, lived for a month. Fasting dogs have lived for 96 to 117 days, and men have survived for over seventy days. Unfortunately, no careful records have been kept of the temperatures at which fasting poikilotherms have been kept and hence no direct comparison with homoiotherms is possible. The former probably can usually endure longer periods without food because their metabolic rate is lower at low temperatures.

Fasting animals, of course, lose weight. In lobsters the organic body constituents fell to one-half their origi-

nal amount after seven months without food. At first protein, carbohydrate, and fat were oxidized equally, but after a time the carbohydrate was exhausted and fat, though present in small quantity, was not used up (Moore and Herdmann, 1914). Starved centrachid fishes lost about one-third of their body weight in two months, but their fat did not fall below .43 per cent of their net weight at the end of the experiment (Pearse, 1925). A starved trout lost one-fifth of its body weight in four weeks at the expense of its protein content. Frogs during starvation did not decrease in weight because of the accumulation of water in their lymph spaces. Most of their organs decreased in weight, but the integument, brain, spinal cord, eyeballs, spleen, kidneys, and testes did not (Ott, 1924). Hibernating woodchucks lost about 3.25 grams per kilo during 110 days (Rasmussen, 1917). In a starving mammal glycogen spares protein if it is available. The nitrogen output decreases during a prolonged fast in a fish or a mammal. This indicates a decrease in metabolism. There is no doubt that such a decrease takes place, for not only does nitrogen excretion decrease, but the oxygen intake and carbon dioxide output is also reduced.

Glands, Enzymes, and Hormones.—The general scheme for the maintenance and control of metabolism appears to be quite similar in homoiotherms and poikilotherms. A fish (Knauthe, 1898) or a turtle (Pearse, Lepkovsky, and Hintze, 1925) requires a certain balance in its food ration and this is apparently quite similar to that which is essential for the proper nutrition of a bird or a mammal. Frogs when fed on white bread develop beri-beri and recover from the disease when supplied with a variety of fruits and insects (Hoffman, 1926). The digestive enzymes of fishes, salamanders, frogs, tur-

tles, and snakes are apparently as effective for digestion as those of homoiotherms and show their greatest degree of activity at about the same temperature, 37 deg. C. (Müller, 1922; Kenyon, 1925). The action of such substances as thyroidin, epinephrin, and insulin is apparently quite similar throughout the series of chordate animals. There are here and there exceptions to these general statements concerning dietary requirements, enzymes, and hormones, but they do not on the whole seem to point to any essential difference between poikilotherms and homoiotherms. For example, vitamin deficiency will not cause scurvy in rats, but pigeons and rabbits are quite subject to such disease. Magath and Mann (1923) believe that the metabolism of carbohydrates is perhaps different in homoiotherms and poikilotherms because they found that after complete excision of the liver the giving of glucose would restore a dog or a goose somewhat, but had no effect on a gar, frog, or turtle. In any vertebrate the mass of protoplasmic substance determines the height of metabolism and the rate and amount of heat production. The rate of metabolism in poikilotherms is in general correlated with the temperature at which it takes place, but in homoiotherms it usually takes place at a rather constant and comparatively high temperature. Enzymes and hormones may modify the rate, but they are not the fundamental cause of it.

Desiccation.—Lack of available water may retard the rate of metabolism. Arthropods and vertebrates commonly prepare for hibernation or aestivation by losing water. A dry rotifer may live in a dormant state for months and, when wet again, complete its life cycle of a few weeks. Desiccation probably causes poor elimination of wastes and inadequate distribution of food and

oxygen to cells. Lack of water also slows down oxidative processes. When about half of an animal's vital limit is exceeded, there is a relative increase in carbon dioxide production (Caldwell, 1925). In land animals which have well developed mechanisms for temperature regulation, climate influences the type of regulation which is used and this indirectly influences metabolism.

Nervous Control of Metabolism.—In all vertebrates the nervous system exerts more or less influence on metabolic processes, and on body temperatures. The ability which nervous domination gives to control temperature is, of course, most important for land animals, which live in a thermally variable environment, but it is present also in vertebrates which never leave the water. The diminution of the oxygen supply has little effect on the rate and strength of gill movements of a Necturus. They are controlled reflexly from the brain, and conditions in the brain centers are the effective agents (Stewart, 1923). There are also "heat centers" in a turtle's brain. "The respiratory rhythm is more powerfully affected by variations in the temperature of the cells composing the respiratory centers than by variations in the activity of the general metabolic processes or in the gases inspired." When temperature of the environment is constant, the amount of carbon dioxide in the blood appears to be the chief factor in regulation (Lumsden, 1924). In homoiotherms, various factors maintain a constant body temperature—insulation, surface cooling through vaso-dilation and evaporation, increased oxidation, etc. The nervous system plays an increasingly important rôle in passing from more primitive to more specialized vertebrates and brain centers take on more complicated relations to temperature regulation. In a mammal the result of the removal of cerebral lobes is a

fall in blood pressure; if the thalamus is also removed there is a further loss of ability to regulate body temperature (Rogers, 1920). The nervous control of metabolism and body temperature may be exercised in indirect ways—such as the stimulation of a gland which gives off a secretion which in turn increases oxidation or changes blood pressure.

Rhythms.—All living things show more or less rhythmical changes in metabolic rate. Such rhythm is one of the fundamental properties of living substance: the viscosity of protoplasm hinders discharge of energy; protoplasm is unstable and trigger action discharges energy during katabolism; endothermic anabolic stages are concerned with reconstruction; katabolism and anabolism must alternate more or less. Periodicity is in part a consequence of the colloidal state (Sager, 1923). Animals are generally adjusted to rhythms. These are characterized by the alternation of periods of rest and activity. They are no more characteristic of poikilotherms than of homoiotherms, except that metabolism in the former is more directly under the control of the environment.

Conclusions.—Poikilotherms do not appear to differ essentially from homoiotherms in the methods employed to carry on metabolic processes. The former show greater variations in metabolic rate because they are more influenced by variations in environment. The latter are more independent of environment because they have controlling mechanisms which permit them to live at a uniform rate if sufficient food is available to supply energy.

CHAPTER VII

FACTORS INFLUENCING BODY TEMPERATURE

The body temperature of an animal may be influenced by a number of factors. Those which are more or less directly related to metabolism have been considered in Chapter VI and will therefore be only briefly discussed again here. Metabolism is, of course, the chief source of the heat which keeps the bodies of animals more or less warm; but other influences such as food, insulation, temperature of environment, adaptation to environmental rhythms, and glandular or nervous control may also be important.

Metabolism.—In a general way the rate of metabolism of poikilotherms varies directly with the temperature of the environment (Krogh, 1914; Powers, 1923; Hall, 1925) and at suboptimum temperatures the opposite is to some degree true of homoiotherms (Pike, 1923). However, poikilotherms have a slight tendency to adjust their rates of metabolism to temperature changes in the environment. A planarian, if changed from an environment of 20 to one of 10 deg. C., at first shows a reduced rate of metabolism, but after two or three weeks returns to about its former rate at 20 deg. C. (Behre, 1918). A turtle which is cooled to 4 to 5 deg. C. shows a check in the gradual decrease in metabolic rate (Baldwin, 1925). Both the planarian and the turtle have a slight tendency to compensate for environmental changes in temperature,

but this is too slow and too limited to permit either to maintain a constant temperature as a homoiotherm does. The ability of fishes to adjust themselves to temperature changes depends on the type of environment in which they have previously lived (Hathaway, 1927, 1928). Overheating of an animal's body may result in acidosis and death (Barbour, 1921). An animal may exercise to produce heat if its body becomes too cool. Bees flap their wings when their hive becomes too cool; a mammal shivers when chilly. In mammals the chemical production of heat becomes important only when the temperature of the environment is as low as 14 to 15 deg. C. (Barbour, 1921; Britton, 1922).

Glandular secretions are potent factors in regulating metabolism and body temperature in vertebrates. In pigeons the thyroid grows larger in autumn, when there is an increase in heat production (Riddle, 1925; Riddle and Fisher, 1925). Less thyroid secretion is apparently needed by tropical animals than by those in cooler regions (Sundstroem, 1922). Glandular secretions, such as epinephrin and thyroidin, may affect body temperatures by changing the water balance in an animal's body (Barbour, 1921). The blood of an animal in an ice bath becomes concentrated (Barbour and Tolstoi, 1921), and is more dilute when the temperature is high (Barbour, 1921). In the tropics mammals have relatively fewer white and more red blood corpuscles (Sunstroem, 1922). Greater concentration of the blood at lower temperatures makes animals better able to endure suboptimum temperatures and permits them to remain active. Among aquatic poikilotherms the character of the water surrounding the body may influence the rate of metabolism, and heat production. For example, a planarian shows a considerable increase in respiratory activity in alkaline

water (Anderson, 1928). The amount of heat given off by an animal varies according to the relation between mass and surface area. On account of this, small homoiotherms require more energy to maintain body temperature than larger. This is not the case among poikilotherms because they expend comparatively little energy to maintain body heat.

Food.—Foods vary in their caloric value and carbohydrates are the best sources of heat. More sugar is needed by animals at lower temperatures (Mansfield and Pap, 1920). It is present in greater quantity in the blood and, of course, furnishes more heat. Associated with this increased consumption there is an increased use of oxidase. Fat and protein may be used for heat production in an animal's body but both are less productive of calories than carbohydrates, and protein is a rather poor source of heat because of the difficulty with which it is broken up and oxidized.

A developing hen's egg uses foods in the following order: carbohydrates, proteins, fats. Needham (1926) discovered this fact and believes that it has phylogenitic significance as an indication of the order in which foods have been utilized by vertebrates in the past. However, Gray (1926) finds that a fish egg derives its energy throughout development largely from protein. He also calls attention to the fact that a land animal must have a considerable supply of water provided for the developing egg. This need for water may be related to the early utilization of carbohydrate in the hen's egg.

Environment.—The temperature of the environment influences the temperature of animals living in it. A poikilotherm tends to have a body temperature which is the same as, or close to that of, the surroundings. At very low or very high temperatures however, the tem-

perature of the body may differ from the surrounding medium. For example, a dormant insect shows a temperature which is practically the same as that of the air about it, but an active insect lags behind as the air temperature rises. When the air is very damp, body temperature may be higher than that of air (Bachmetjew, 1901). Desert insects may show a body temperature as much as 15 deg. C. below that of their surroundings. Many animals in hot situations hide during the day or during the dry, warm season and become active when the direct rays of the sun are not present. In cool situations the opposite is often true. Some animals show daily or seasonal rhythms in heat production and body temperature. Even such a specialized homoiotherm as a bank swallow may show considerable daily fluctuation in body temperature (Stoner, 1926). Many homoiotherms pass through long periods of rest, during which they lose their powers of maintaining constant body temperature.

Insulation.—Poikilotherms during cold periods are obliged to resort to situations where they will not freeze. They commonly burrow into the soil or into mud where the decay of organic materials prevents freezing; they hide away in springs, caves, under leaves, and in logs and hollow trees. They seek insulation or a warm situation in their environment. The skins of reptiles protect them well from loss of water, but not so well from loss of heat. Insulation for conserving heat is generally not present on the exteriors of animals, except among homoiothermic vertebrates. Hair, feathers, and fat are the materials employed and they show more or less adaptation for particular situations and localities. Animals in the tropics are generally thin and those in frigid regions commonly have a thick layer of subcutaneous adipose

tissue. The thickest furry and feathery coats are found in the arctic and antarctic. Well-insulated homoiotherms are often obliged to exercise some care to prevent their bodies from becoming overheated and many have developed special cooling mechanisms, which usually produce their effects by evaporating water and permitting the ready loss of heat from the skin, lungs, or alimentary tract. Most of the large animals in the tropics avoid the direct rays of the sun.

Nervous Control.—The regulation of body temperature in man is largely under the control of the nervous system, which contracts or expands appropriate blood vessels so that liquid is sent to the skin or to the internal organs, causes loss of liquid from the blood to the tissues, stimulates glands to secrete water or substances which facilitate the production of heat through chemical action, and acts in other ways. A normal dog in an ice bath shows a concentration of the blood, but a dog with a transsected spinal cord does not. In mammals and birds generally, temperature regulation is dominated by the nervous system. In other vertebrates the nervous system also exercises some control, but this control is not complete enough to result in the maintenance of a constant body temperature. In invertebrates the same type of regulation appears to be present, but it takes the form of slow acclimating changes which require days or weeks for their completion (Behre, 1918; Hathaway, 1927). Cooling mechanisms for the control of body temperatures are present in insects, and probably in other terrestrial arthropods, in birds, and in mammals. In homoiotherms such mechanisms are concerned chiefly with peripheral vasodilation and the evaporation of water from the skin, lungs, or oral cavity. They are largely under the control of the nervous system.

Conclusions.—The body temperature of animals is influenced by variations in metabolism, food, the transfer of liquids, evaporation, insulation, glandular secretions, the temperature of environment, and surface mass relations. The regulation of body temperature in homoiotherms appears to differ from that in poikilotherms in degree and somewhat in kind. In the former it is made more rapid and effective by insulation, nervous control, and better mechanisms for the chemical production of heat and for cooling.

CHAPTER VIII

THE MECHANISMS OF TEMPERATURE REGULATION IN HOMOIOTHERMS

The preservation of life in a homoiothermal animal requires the maintenance of a constant temperature, though the external and internal conditions may vary greatly and may tend to warm or cool the body. A variation of a few degrees in the internal temperature of a higher mammal may result in death. Normally, little variation occurs. Such constancy results from the adjustment between characteristic temperature regulating mechanisms which are present in the homoiotherms: heat is produced continuously and rapidly and is dissipated at about the same rate. The living organism must adjust heat production and heat loss in such fashion that the temperature of the body cells is maintained near their optimum. Such regulation is termed *thermotaxis*, or the balance maintained between the two mechanisms:

1. Regulation of the loss of heat. This is termed physical heat regulation, or *thermolysis*.
2. Regulation of the production of heat. This is the chemical heat regulation, or *thermogenesis*.

Thermogenesis.—The metabolism of the poikilotherms is influenced by temperature in such a way that lower temperatures result in low rates of metabolism and high temperatures in high rates. In general the Van't Hoff law for chemical reactions is followed. This is

evidently not true in the case of the homoiotherms. Many experiments show that a fall in the temperature of the environment of a warm-blooded animal induces a higher rate of metabolism and with a rise in temperature the reverse seems to be true until the environmental temperature reaches about 35 deg. C., but above this temperature there is again an increase.

Thermogenesis operates in the body of a homoiotherm to compensate for heat lost by radiation and conduction. Since the temperature of a homoiotherm is usually above that of its environment, it will constantly lose heat. The amount of heat lost will be determined by the factors influencing radiation and conduction. These have been described in Chapter IV. Thermogenesis is thus in a sense a curative mechanism, since it furnishes the means whereby heat is produced in the body to compensate for that lost.

The energy which is required to maintain life processes at any given temperature and the additional heat which is necessary with a fall in the temperature of the surrounding medium are directly derived from metabolic processes. Heat is liberated through oxidation, either by voluntary muscular exercise, reflex muscular contractions such as shivering, or by the transformation of food. Oxidations take place in the tissues and the seat of heat production is therefore in them. The greater part of the body heat of a mammal is produced in the muscles. Seventy to 80 per cent of the energy liberated during a muscle contraction is in the form of heat. About one-half the active tissues of an average vertebrate are muscular and, as the muscles are by far the most active of the tissues, a great amount of heat must be furnished by them. Some of the glands, especially the liver, are also important sources of heat.

Supplemental to the production of heat by oxidation during periods of falling temperatures, either in the environment or in the blood itself, are certain physiological adjustments on the part of the organism, some retard heat loss and others hasten the dissipation of heat. Among these are: (1) cutaneous vaso-constriction, which decreases loss of heat through the skin; (2) reduction in blood volume, which apparently permits the constriction of peripheral blood vessels without excessive engorgement of those on the interior; (3) behavior which results in the aggregation of groups of individuals or "huddling" reflexes which in cold surroundings reduce the area of exposed body surface, and thus check loss of heat by radiation and conduction.

Thermolysis.—The mechanisms for regulation of heat dissipation are mainly employed when there is danger of overheating an animal's body. The dangers from supraoptimum temperatures usually arise from within the body rather than from the environment. A rise in temperature either in the blood or skin results in the heat center in the central nervous system stimulating an increased heat dissipation which may be brought about by the following physiological means: (1) hyperpnea, or panting, (2) cutaneous vaso-dilatation, (3) evaporation of moisture from exposed moist surfaces, (4) decreased muscular exertion, (5) maximum exposure of body surfaces, as in outstretched animals during hot weather.

Physical thermolysis is accomplished by radiation, conduction, and water loss. It has been estimated that at ordinary room temperatures about 75 per cent of the heat produced by the human body is lost by radiation and conduction and 25 per cent through the evaporation of water from the surfaces of lung and skin. At higher

surrounding temperatures this proportion changes, relatively more heat escaping by evaporation and less by radiation and conduction.

High temperatures usually cause animals to breathe more deeply. Animals, such as the fur bearing mammals which lack sweat glands, show the most marked hyperpnea. When a dog extends its tongue and pants, the loss of water from its body is greatly increased. Animals subjected to sources of radiation from which they absorb heat often show pronounced hyperpnea.

Blood volume is increased when the body temperature rises and this acts as a means of preventing vasodilatation and also maintaining a sufficient supply of water for sweat secretion.

When the external temperature is high or when thermogenesis is great, as in muscular work, the cutaneous blood vessels dilate, those within the abdomen constrict, and a larger volume of warm blood is thus sent to the surface to be cooled. The cooled blood is returned to the interior to take up more heat and is again returned to the skin. Thus a great flow of blood through the skin is obtained and this results in a maximum discharge of heat by radiation and conduction. On a cold day the reverse takes place, so that the warm blood is restrained from circulating too freely through the skin where more heat would be lost. A rabbit depends chiefly on its vasomotor activity for temperature regulation, as it does not possess a satisfactory water reserve. This is likely true with other herbivores although no evidence seems to be available. Certain drugs may paralyze the vasomotor mechanism. For example, an animal under the influence of alcohol feels warmer and loses more heat than a normal individual.

Thermolysis is voluntary to a certain extent, for by

artificially covering the body with clothing, by taking advantage of shelter in homes, by warming the food and drink taken into the body, and by heating the atmosphere with which the body comes in contact, man protects himself against a too great loss of heat and decreases to a large extent the necessity of relying upon the involuntary, and subconscious, means of temperature regulation.

Evaporation of Moisture.—When the temperature of the body is like that of the environment of an animal, the heat lost by radiation and conduction will be exactly balanced by the heat absorbed. As the environment attains a higher temperature than the body a means of heat elimination by conduction or radiation become inadequate and thermolytic means are employed; *i.e.,* the evaporation of water from surface of the organism.

The quantity of heat lost by evaporation of moisture depends upon several factors:

1. Humidity of circumjacent atmosphere.
2. Temperature gradient between body and environment.
3. Velocity of movement of circumjacent atmosphere.
4. Effective area of moist surface exposed.
5. Color of moist surface exposed.

The amount of moisture in the air affects its cooling powers. If the air is saturated, it can obviously contain no more moisture and consequently no water is lost by the organism. Also moist air is a much better conductor of heat than dry air and heat lost by conduction is at its maximum in a humid atmosphere. The former factor plays an important part when the surroundings are warmer than the animal, the latter acts when the environment is colder.

The temperature gradient between the surrounding medium and the animal limits the amount of heat lost by evaporation. The greater the gradient, the stronger the

stimulation of the mechanism for sweating. Currents of air over the surface of an animal remove the water vapor, bring dry air in contact with the skin, and thus decrease the partial pressure of the gas next to the skin. In a strong wind the partial pressure is at its minimum in the layer of air next to the body. The drying effect of winds is more or less independent of their temperature but is directly related to their water saturation deficit.

The effective area of surface exposed to cooling depends in great measure on the state of the superficial blood vessels. Dilatation greatly increases the effective surface; constriction, the converse.

The effect of color is merely a matter of differential absorption of radiant energy which produces local heating in proportion to the amount of energy absorbed and so causes a more or less rapid evaporation. The black moist nose of a dog is much cooler than a similar dry, white area.

There are about 2 to 3 million sweat glands in the entire skin of a man. The number apparently varies considerably in different species of mammals; the dog, for example, has none. The volume of secretion among species which possess sweat glands is also variable and there is a marked variation among the individuals of a single species. In man it may vary from a minimum of 700 ml. per twenty-four hours to three times that amount. Whether volume changes are due to changes in number of active glands or to variations in the output of individual glands is not known. Adolph (1923) has shown that when an active body is exposed to high external temperatures the quantity of sweat is a linear function of the "effective" skin temperature. It appears therefore that as the limit of heat dissipation by conduction and radia-

tion is approached (at about 32 to 33 deg. C.) vaso-dilatation has reached its maximum effect and beyond that impulses from the heat center can only accomplish an increased heat loss from the body by augmenting sweat secretion. All the skin changes resulting from excitation of the heat center operate harmoniously to favor or impede heat dissipation under normal conditions.

Water is very well fitted for the requirements of temperature equalization and regulation in animals. Its mobility permits it to circulate freely and rapidly in the organism. Henderson (1913) attributes the fitness of water for temperature equalization and regulation to three qualities: (1) great specific heat, (2) large amount of heat required for evaporation, and (3) good thermal conductivity. The first promotes the storage of heat; the second permits very rapid elimination of heat when the environmental temperature exceeds that of the body; the third contributes to the rapid equalization of heat within the immobile tissues of the body and minimizes the possibility of injury from local overheating. The cooling power of water is great. One liter of water requires 580 kilogram calories for its vaporization. This factor makes water of extreme importance in heat loss.

Water plays a significant rôle in the maintenance of constant temperature in homoiotherms. It constitutes about 70 per cent of the substance of an animal's body and is one of the most abundant and available constituents of the environment. Aside from its function in the regulation of temperature, it is fundamentally important in the other physiological processes of the body. Water, in consequence of its peculiar properties and abundance in nature, is important in the regulation of the temperature on all parts of the earth, in both air and water, as well as in organisms.

The Thermal Nerve Center.—Since many means are brought to play in organisms for the maintenance of a constant body temperature and especially since a variety of nerves—vasomotor, muscular, secretory—are involved, it is apparent that a coordinating center is required. Experimental evidence obtained by Barbour (1921) and others indicates that such a center exists in the *corpus striatum.* The gain or loss of heat by an organism depends upon many interwoven factors such as blood-content, colloids, water-content, various ions and metabolites, and other physiological factors. These probably maintain a fair degree of constancy in the poikilotherms. But temperature regulation must depend upon something more. It occurs in those species which have a highly developed nervous system and only when in those particular species the nervous system has reached a certain stage of development in each individual. Therefore one concludes that in the evolution of the temperature regulation a new function has been added and that the nervous system has gained control of those physiological processes which affect the gain and loss of heat in the organism. Barbour (1921) clearly demonstrated that the application of heat or cold to the anterior end of the corpus striatum by means of a small metal tube through which water of various temperatures was circulated, caused marked changes in the body temperature of the animal. When cold objects were applied to the nerve center, the rectal temperature rose and shivering and vaso-constriction of the skin were also observed. If objects having a temperature above that of the body were applied, a fall in rectal temperature and muscular relaxation and dilatation of the skin blood vessels occurred. These results have been confirmed by several later investigators. Barbour (1921) states that

the left "heat center" is more strongly developed than the right in the rabbit. Barbour and Prince (1914) found that local applications of heat to the heat center caused diminution in the production of carbon dioxide and in the consumption of oxygen. Cooling the center reversed these effects.

Effects of Decerebration and Spinal Cord Sections on Thermoregulation.—The importance of the brain on heat regulation has been demonstrated by the removal of the cerebrum. Rogers (1919) has shown that the ability to regulate body temperature is lost in decerebrate pigeons when the optic thalamus has been injured. Freund and Strosmann (Barbour, 1921) sectioned the cord at various levels and found that, while normal rabbits withstood environmental temperatures of 6 to 31 deg. C. with no appreciable change in body temperature, those with the cord sectioned were poorly regulated. Rabbits which had the dorsal cord sectioned, could regulate their temperature fairly well between 18 and 31 deg. C., but were ineffective beyond those limits. In rabbits with the cervical cord sectioned a poikilothermal condition obtained in environments varying from 19 to 33 deg. C. Freund (Barbour, 1921) has found more recently that if in addition to the dorsal cord operation a double vagotomy just below the diaphragm is performed an animal becomes poikilothermic to essentially the same extent as those with the cervical cord transsected. He concludes that this is likely due to the severance of the sympathetic fibers.

Garrelon and Langlos (Barbour, 1921) suggested a "polypnea center." In corroboration of that idea Nicolaides and Dontas (Barbour, 1921) have found that heat polypnea cannot occur if the medulla is separated from

the brain, although the ordinary respiratory movements are not disturbed.

It would seem, therefore, that, although there may be some grounds for believing that the nervous control of heat regulation is widely distributed, the evidence points to the conclusion that the temperature regulation of the mammals is chiefly coordinated at the base of the brain in the corpus striatum.

The Temperature Sense.—The sensations of heat and cold which an animal experiences from time to time are caused by changes in the temperature of the skin. Innumerable nerve endings are distributed over the skin and these, when stimulated, evoke sensations of heat or cold. Each responds to but one type of stimulus, *i.e.*, a warm object applied to a heat nerve ending elicits a sensation of warmth. It has little or no effect upon a cold spot. The reverse is also true. The sensitivity of the human skin to temperature changes is very acute.

It is an interesting correlation that the main channel of heat elimination is through the skin, that the skin is the only part of the body directly exposed to the environment, and that the skin has widely distributed through its outer layer the temperature sense organs. The skin is the first part of an animal's body to respond to temperature variation in the environment. The physiologic stimulus to the thermic end-organs is the passage of heat through the skin from the interior to the surrounding medium. Impulses are sent to the heat center. Thus the heat center anticipates changes in actual blood temperature by compensatory reactions to changes in the skin temperature. Consequently if radiation and conduction are continuous and uniform, the end organs adapt themselves to the temperature of the surrounding medium.

If there is a sudden rise in the external temperature caused by some factor which diminishes the loss of heat, the temperature of the skin will rise, the end organs will be stimulated, and the sensation of warmth is developed. Conversely a fall in temperature stimulates the receptors for cold. The afferent impulses in either case stimulate the heat center to the proper activity resulting in a regulation through heat dissipation or conservation. Since changes in skin temperature would eventually influence the general body temperature if not compensated for, the temperature sense organ undoubtedly serves a useful purpose in temperature regulation.

Fever.—One of the most striking aspects of many pathological disturbances is a rise in body temperature, a condition known as fever. This increase in heat may be the consequence of a greater production than can be lost through the normal channels, or of a lack of regulation of the loss of heat. Most investigators hold that, although there may be a slight increase in the production of heat in fevers, this is too small to account for a rise of several degrees in the body temperature; in fact, many physiologists now believe that the rise in basal metabolism during fever is to be regarded as a result of the rise in temperature, rather than as a cause.

Fevers are apparently secondary factors in infections. Toxins act to increase the affinity of protoplasmic colloids for water with the result that the blood volume is reduced. This effect is assumed to be localized mainly at the body surface and leads to a cooling of the periphery and the sending of afferent impulses to the heat center. Thus the thermolytic mechanism is brought into play, without regard to the actual heat equilibrium.

The Endocrines and Temperature Regulation.—The endocrines unquestionably have an influence on the tem-

perature regulation of homoiotherms. The thyroid has marked effects upon the oxidative processes and also influences heat production. Mansfield and Pap (1920) emphasized the relationship between heat regulation and the control of the thyroids over oxidation. It has been observed also from clinical practice that thyroidectomized animals regulate their temperatures with difficulty. The more pronounced disturbances of heat regulation seem to occur most commonly and most strikingly in connection with diseases of the thyroid gland. In myxedema the body temperature often drops far below normal. In exophthalmic goiter, hyperthermia is commonly reported. Structural variations in the thyroid which vary according to environmental temperatures are described by Barbour (1921).

The influence of insulin upon body temperature has been observed by Cassidy, Dworkin, and Finney (1926). These investigators studied the relation of sugar metabolism to hibernation in mammals and found that if insulin was injected and the blood sugar thus decreased, the shivering reflexes were absent when the animal was subjected to cold.

Erection of hairs, ruffling of feathers, constriction of peripheral blood vessels, and increase of blood sugar have been mentioned as responses of homoiotherms to cold temperatures. The investigations of Cannon, Querido, Britton, and Bright (1927) indicate that adrenalin brings about such responses and furnishes a means for protecting the organism against cooling. They found that by producing a heat debt in animals an increased activity of the medullary portion of the adrenal gland was induced and that this led to an extra output of adrenin, which in turn hastened combustion. They also believe that heat is produced in the body without shiver-

ing as a result of the direct increase of metabolism by adrenin and that this compensates for heat loss.

Some observations reported by early workers indicate that the pituitary decreases in size during hibernation but enlarges again and becomes more vascular when an animal awakens. Rasmussen (1921) however believes that changes in the pituitary are not a cause of hibernation. He bases his conclusion on experiments with a large number of woodchucks. The pituitary hormone exerts a marked influence on the water balance of the body (Rowntree, 1922) and therefore would affect the regulation of bodily temperature. Falta (1923) states that hypophysial dystrophy is always accompanied by abnormally low body temperatures. The hypophysis apparently promotes temperature regulation on account of its influence on the nervous system.

One may conclude from the observations made in the study of endocrinology that hormones doubtless play an important rôle in the control and maintenance of the body temperature. Since little is known of the reciprocal action of hormones, the exact part they play is still somewhat hypothetical. Future investigation will likely add much to knowledge of their mode of action and this is a promising field for study.

CHAPTER IX

GROWTH AND LONGEVITY

The growth of any organism is, of course, the result of many interdigitating factors. An animal to increase in size must have food to supply building material. It must have a body temperature which permits anabolic reactions to proceed at such a rate that they exceed the destructive changes which are essential for living from day to day. It must be free from parasites or diseases which sap its vitality. Growth also depends on a continual balance between an animal and its environment. Food must not only contain material but must furnish a proper balance of calories, amino acids, and vitamins. Environmental temperature should not only fall within the limits where metabolism and growth may occur, but, to permit an animal to really flourish, should vary so that growth receives healthful stimulation. Growth is a complex phenomenon which through metabolic wasting and waxing results in a net increment in size.

Rate of Growth.—The rate of growth of animals is usually progressively slower with increasing age (Brody, 1927). There may be seasonal fluctuations or variations associated with progression through the life cycle, but in general the metabolic rate gradually runs down. Some animals grow rather slowly and at a rather constant rate, and others increase largely during intermittent periods of building.

Rubner (1924) in his admirable studies on metabolism

and growth has computed the times required for various vertebrates to double their weights during early growth and gives the figures shown in Table II. The gestation period of the dog and cat are 56 and 63 days; the comparable development of the pike requires 574 days. The rate of growth of a dog is comparable to that of a pike after it is dependent on its own resources for the manufacture of food; *i.e.,* after it has ceased to depend on food supplied by its mother. At 16 deg. C. a mammal requires 800 calories per kilogram of body weight per day; a fish at the same temperature needs only 30.8 kg.-cal. per day. A pike is slower but for the same amount of growth requires about the same amount of energy. A fish weighing 1.75 grams needs 39 calories in 24 hours; a mouse of the same size needs 997 calories in 24 hours. The mouse consumes 25 times as much as the fish.

TABLE II

Time Required for Animals to Double their Weights, as Determined by Rubner (1924)

Doubling	Cat			Dog			Pike		
	Weight, Grams	Time, Days	Energy Needed	Weight, Grams	Time, Days	Energy Needed	Weight, Grams	Time, Days	Energy Needed
Birth weight	87	0	0	225	0	0	70	0	0
1	174	7.5	3235	450	10.0	2983	140	274	3267
2	348	12.0	3975	900	12.5	3068	280	303	2350
3	696	22 0	5295	1800	22.5	4010	560	336	2773
4	1392	53.0	9587	3600	40.0	6180	1120	613	3598
5	......	......	......	......	......	......	2240	1179	5162

Rubner (1924a) has made further studies which relate especially to amphibians and reptiles and makes a general comparison between homoiotherms and poikilotherms. Growth begins with a considerable amount of water in body cells and a variable colloid content. As growth progresses, water gradually decreases. Hor-

mones and endocrine secretions play an important rôle, especially in homoiotherms. Larger animals in general require less energy than smaller, on account of surface-mass relations. Fishes have little physical regulation of body temperature because they live in water. Amphibians commonly regulate their body temperature through their lungs and skin. The growth of homoiotherms and poikilotherms is similar. Energy requirements depend on size and rate of growth, and rate of growth in many cases depends on the temperatures at which metabolic reactions take place.

Mammals may differ among themselves in rate of growth. Brody (1928) has recently made careful studies of several domestic animals and compares them with man. "The length of the juvenile period in man is about 10 years (4 to 14 years). This relatively enormous length of the juvenile period appears to be the most distinguished feature of the growth curve of man. . . . In the curve of man, the major inflection (at puberty) occurs when the body weight is, roughly, two-thirds of the mature weight; in other animals it occurs when the body weight is, roughly, one-third of the mature weight. . . . There are no radical quantitative or qualitative differences between the growth curves of man and other animals during the phase of growth following puberty. . . . If the percentage rate of growth for a given group of children is relatively low during earlier ages, then there is usually an acceleration between 12 and 15 years; if it is high, there is no acceleration. The pubertal acceleration, when present, appears to be in the nature of a compensatory growth for earlier deficiency. . . . It should be said that growth in length takes place at an approximately constant time rate when growth in weight takes place at a constant *percentage* rate. This is evi-

dent from geometrical considerations when growth in length is strictly terminal. It is also evident from physiological considerations; constant percentage rates of growth in volume and constant time rate of terminal growth both imply that the physiological environment with respect to the growth-limiting process remains constant." MacDowell, Allen, and MacDowell (1927) have compared the growth rate of the mouse, guinea pig, and chick. They conclude that "growth of different animals may be compared more accurately if, instead of either birth age or conception age, embryo age is used."

It is difficult to compare the growth of homoiotherms and poikilotherms and often difficult to compare that of animals in the same class or order. A guinea pig or a snake is able to shift for itself soon after birth; a robin or a child has a long youthful period during which it is nourished and protected by its parents.

As has been stated, some types of animals grow at a rather constant rate; others grow in spurts; and others grow rapidly during youth and then more slowly. A painted turtle (*Chrysemys belli*) doubles its weight and length during its second year of life, but after twelve years increases at one-thirtieth the rate for the first two years (Pearse, 1923; Pearse, Lepkovsky, and Hintze, 1925a). The sea turtle, *Caretta caretta,* at hatching weighs 20 grams; at 4¾ months, 800 grams; and at 3 years, 19 kilograms (Parker, 1926). The Pacific striped bass grows 150 per cent in length during its second year, but during its twelfth year of life, only two per cent (Scofield, 1928). A carp may weigh 500 grams when it is two years of age and then gain 750 grams between the beginning of May and the middle of August, when it may attain a weight of 1250 grams (Pütter, 1909). However, a fish living in natural conditions often does not

grow to the full extent of its capabilities. A particular species which occurs in two lakes only a few miles apart may be uniformly of small size in one lake and large in the other (Pearse, 1918; Pearse and Achtenberg, 1920). In nature, animals in particular habitats may never be able to exercise their full capacity to grow. Peterson (1918) found that in one locality off the coast of Denmark the plaice did not grow for two-thirds of a year, but if individuals were transferred to another locality they grew at normal rates. Sundstroem (1922) kept mice in an "artificial tropical" environment where there was little circulation of air and where other conditions were monotonous. He found that they did not grow as well as mice reared where conditions were variable.

Methods of Growth.—While in general percentage additions become less and less as an animal grows, there are usually more or less intermittent periods of rapid and slow growth which are characteristic of species and of individuals. Young tissues grow fastest and perhaps old animals grow more slowly because they come to contain a considerable bulk of inert, differentiated, and comparatively stable tissues. "Accompanying differentiation there is, therefore, a decrease in the activities of metabolism" (Beer, 1924). An animal may, however, show an increased rate of metabolism during degrowth, or decrease in size.

Robertson (1923) in his comprehensive work on growth observes that most animals increase in size by spurts with periods of slower growth between. He believes this is due to an autocatalyzed process. He found that there were usually three growth cycles. Robertson believes that the rate of growth reactions depends on (1) the specific reaction velocity of the process, (2) the concentration of autocatylist, (3) the concentration of

raw food materials, and (4) the rate of nuclear synthesis. He characterizes the process which takes place at the slowest rate—and therefore limits all others—as "the master reaction." From his point of view, growth may be slowed up by the exhaustion of autocatylist or food, or by the accumulation of products.

Brody (1927) has made extensive studies of growth. "Growth curves consist, in all cases, of two major segments. The first major segment is, in the case of higher animals and plants, made up in turn of several (probably five) shorter segments during each of which growth takes place at a constant percentage rate. The transitions between the successive stages are abrupt, the abruptness being of the same order as that of metamorphosis in cold-blooded animals. . . . The junction between the two major segments occurs at puberty in animals and flowering in plants. . . . The two major segments of the inflection are not symmetrical about the major inflection. The slope of the segment following the inflection is always less than the slope of the segment preceding the inflection. The major inflection does not occur in the center of the growth curve." At the beginning, growth may be 100 to 200 per cent per day. The body weight may be doubled in from 7 to 17 hours. Two months after conception the increase in man is about 8 per cent per day. "Dr. Stockard called attention to the fact that the peak in the mortality curve of the chick at 5 days is the counterpart of the peak in the prenatal mortality curve in man at 3 months. This is the junction between the embryonic period (formation of organs) and the fetal period (enlargement of body and organs)." The nature of the growth in the two periods is quite different, hence it is not strange to find a high mortality at the time of transition from one to the other.

Growth and Temperature of Environment.—The growth of poikilotherms and of young homoiotherms is limited by the temperature of the environment. A young bird or mammal must be kept warm in a nest, marsupial pouch, or uterus if development is to follow a normal course. Yet such development does not necessarily need to take place at temperatures which are near those of the bodies of the parents. An egg may mature in the body of a hibernating frog and an embryo may continue to develop in a hibernating mammal. After leaving the body of the parent a frog's egg may rest in water beneath ice and develop normally as the temperature rises. The eggs of various reptiles are commonly buried where they are heated by the rays of the sun, as on warm hillsides, or where they may be heated by decaying organic matter, as in rotting logs. A hen's egg may remain cool for some time before development begins. It can later endure for short periods temperatures which are below the body temperature of the hen and still develop into a normal chick.

Homoiotherms in gaining the ability to maintain a constant temperature through metabolic activity and other means have also become able to provide a favorable temperature for the development of their offspring. The eggs of frogs developing at 8 deg. C. require 30 days to reach the same stage which they will reach in 8 days at 21 deg. C. (Barthélémy and Bonnet, 1926).

Determinate Growth.—Some animals grow less and less as time goes on but appear to continue indefinitely, others cease to grow when they reach maturity. In general indeterminate growth is more characteristic of poikilotherms than of homoiotherms. The prolonged and more or less indeterminate growth which occurs among fishes, amphibians, and reptiles is characteristic of

species or individuals which have long lives. Among homoiotherms there is usually a rather sharp demarkation between youth and maturity.

The reasons why animals cease to grow are not certainly known, but several theories have been advanced. Continued growth is perhaps normal for all living things but it is stopped in some cases by other factors. Differentiation may result in the production of such a bulk of inert tissues that growth is no longer possible (Robertson, 1923). Growth-stopping substances may increase with age (Beer, 1924). These may be waste products, hormones, or other substances which inhibit cell activity. Metabolic gradients may be concerned (Child, 1915). Regions where a high rate of metabolism obtains dominate those regions of lower rate. When a part gets too far from the dominant region for effective control, growth ceases. There may be a lack of growth-promoting substances, such as available food or autocatylist (Robertson, 1923).

Growth in homoiotherms is apparently not fundamentally different from that in poikilotherms, but the adjustments associated with a high degree of somatic differentiation, the prolonged care of young by parents, and the maintenance of constant temperature have apparently led to determine growth. The body of a homoiotherm has, through differentiation, come to have a greater segregation of the various functions of its life cycle, and the growth period is rather sharply differentiated from the reproductive period.

Longevity.—Protozoa, as individuals, may live for a few hours, days, or months. Invertebrates exist as individuals for a few months or perhaps even for several years. Anemones have been kept alive for more than 60 years and corals have been known to live for 20 to

30 years, but the animals having the longest lives are vertebrates, and these have also been most successful in invading the most variable habitats on land and in fresh water. The arthropods and vertebrates are the dominants on land, where the rarity of the atmosphere makes it possible to move swiftly and the constant presence of an abundance of oxygen permits a rapid rate of living. The arthropods have never as individuals attained constant body temperature, though a few species of ants and bees as colonies maintain a rather high temperature. If the arthropods possessed long life and the ability to maintain constant temperature, they would perhaps excel the vertebrates.

Fishes have been known to live for more than a hundred years (Günther, 1880). The giant Japanese salamander has lived 52 years; Amphiuma, 27; Siren, 25; Hyla, 20; Rana, 16; and Bufo, 13 (Fowler, 1925). Many reptiles live to great ages. Ditmars (1902) estimated the ages of certain giant tortoises at 350 and 400 years. Other types of tortoises have been known to live for from 60 to 143 years (Babcock, 1928). Many birds and mammals live to great ages. Among vertebrates generally, larger species of animals live longer than smaller types of comparable structure. Animals which grow quickly to a rather definite size are usually comparatively short-lived. Mammals which live long lives commonly breed less frequently than smaller, short-lived types.

Ecologically, longevity is related to the balance of life in any locality or habitat. It is correlated with food supply, favorable seasons for feeding and growth, available space in which to live, time required to reach maturity, and other factors. By acquiring ability to live long, vertebrates are able to have the lives of parent and offspring overlap and thus heritages, such as particular

homes or customs, which are not part of the somatic equipment of each individual, may be passed on from generation to generation to a greater degree than among short-lived animals.

Long life and the ability to maintain a constant temperature have given birds and mammals great advantages over other animals. They live without any breaks in their activities and thus have better opportunities for gaining and profiting by experience. Continuity of living at a constant temperature and a high rate of metabolism have probably thus been the chief factors which have made it possible for them to become wiser.

CHAPTER X

PERIODIC FLUCTUATIONS IN BODY TEMPERATURE

Homoiotherms may show periodic fluctuations, diurnal or seasonal, in body temperature while in a state of normal health. They may also show variations in body temperature which are independent of extracorporal or periodically recurring influences during certain phases of their life cycle. No intrinsic periodic fluctuations are apparent in the poikilotherms, obviously because the environmental temperature is the determining factor.

Diurnal Variation.—The diurnal variation in the normal body temperature of animals has been little studied. In man its usual range is about 1 deg. C. The maximum temperature usually occurs about 4 to 6 p. m. and the minimum about 4 to 6 a. m. With these diurnal changes in temperature are associated parallel oscillations in the rate of metabolism, as shown by the elimination of carbon dioxide. While such variation may be partially accounted for by the movement and tonus of the muscles occurring during the waking hours, an inherent cycle apparently exists. Benedict's (1904) observations made on night workers showed that adjustment to change in the daily routine was incomplete even after a period of years. Gibson (1905) found that his diurnal metabolic variations maintained a parallelism with the daylight and darkness while he traveled around the world. It

seems that while a diurnal variation occurs in birds, it can readily be changed by changing the time of activity. Owls and other nocturnal birds show their maximum temperatures in the night.

It is an interesting speculative consideration that maximum and minimum temperature oscillations in the bodies of animals coincide with those of the sea. The maximum temperature of the sea is late in the afternoon while the minimum is late in the night, near dawn. The normal variation in shallow waters is similarly about 1 deg. C. It appears possible that there is in the body temperature of the homoiotherms an indication of the temperature of the sea at the time when their ancestors migrated from the water to the land. If this is true, a homoiotherm, although it at present maintains a constant temperature much above that of its surroundings, has mechanisms for keeping pace with temperatures to which the ancestors were accustomed or perhaps to those which they found advantageous in their original marine environment.

Age.—At birth the temperature of the homoiotherms varies with the species. Some are more affected by environmental temperature than others. Young marsupials, such as opossums, with their undeveloped nervous system, have little resistance to temperature changes in the surroundings. On the other hand the young of the guinea pig will soon after birth maintain its body within a fraction of a degree of that of the mother. A human infant has a slightly higher temperature at birth than its mother. During childhood the body temperature gradually falls to that of the adult. In old age the temperature rises as a rule and attains a maximum at about eighty years. The young of certain birds are practically poikilothermic at hatching (Kendeigh and Baldwin,

1928) but gradually become homoiothermic as they grow older.

Hibernation.—Hibernation is a resting state during which animals exist in a more or less torpid condition. It is a response usually associated with cold, in contrast to other states of inactivity such as aestivation, which is a response to warm, dry periods, and to inactivity which occurs at certain periods in the life cycle independent of temperature variations, such as the pupal stage of many insects.

Hibernation is a term generally applied to a torpid state which occurs concomitantly with low temperatures and is widely distributed through various groups of the animal kingdom. Protozoans, rotifers, annelids, and copepods commonly rest within cysts; snails close the mouths of their shells and remain dormant; certain fishes inclose themselves in cocoons of mud and slime; many poikilothermal vertebrates burrow in order to remain torpid through cold seasons. Among the homoiothermal animals only a few representatives of the mammals hibernate; namely, certain insectivores, bats, rodents, and carnivores. There are no hibernating birds, but many of them evade unfavorable temperature conditions by migrating.

Whether hibernation is directly induced by low temperatures or not is still a controversial question. Many investigators believe that it is more likely a response to lack of food and that temperature is only a coincident factor. Animals like squirrels prepare for hibernation either by storing up food, which they consume at intervals when they awake, or by fattening before they become dormant. Pembrey (1895) has shown that there is an extraordinary low respiratory quotient in hibernating mammals. This means that there is a conversion of fat

into carbohydrates. The fact that a hibernating marmot increases in weight during hibernation indicates that oxygen is actually retained. A marmot's respiratory quotient under such conditions is about 0.30.

In a study of hibernation in the ground squirrel, *Citellus tridecemlineatus* (Mitchell), Johnson (1928) showed that during the period of torpidity the body temperature fell as low as 0 to 2 deg. C., which was within one degree of the surrounding temperature. During the period of hibernation a ground-squirrel sometimes loses 40 per cent of its body weight. Johnson also observed that the respirations dropped from 100–200 per minute in active animals to 1–4 in torpid animals. The rate of heart beat likewise ranged from 200 to 350 per minute in the active animals but decreased to a minimum of 5 beats per minute in hibernating individuals. These observations indicate a very low metabolism during hibernation and a close approximation to the poikilothermal condition during the cold seasons.

Hibernation is a condition apparently fairly well distributed through a variety of mammals. Martin (1903) observed *Echidna* in hibernation, during which it took neither food nor water and showed a body temperature which followed that of its surroundings within 0.5 deg. C. Animals remained in a torpid state for as much as 4 months. The production of heat in *Echidna* was proportional to the difference in temperature between animal and environment.

Mammals are descended from poikilothermal animals. Some have reached a less perfectly homoiothermic state than others and perhaps have some imperfections in their heat regulating mechanism. These have made a virtue of necessity by becoming hibernators. They cannot sustain the temperature at the level required for a continu-

ance of everyday life, so they relapse into somnolence and inactivity. They pass into a state of imperfect homoiothermism, which is very economical of energy and during scarcity of food may permit them to withstand unfavorable conditions in their environments. While torpid they slowly burn away the energy sources of their bodies to keep up a modicum of animal heat, thus compensating for the inevitable loss. Hibernation is a condition which apparently obtains in certain groups throughout the course of mammalian evolution. It seems to be a persistent, adaptive reaction of survival value.

CHAPTER XI

BEHAVIOR AND BODY TEMPERATURE

Behavior is the term used to characterize the movements which animals make in response to stimuli. In general behavior shows adaptation in that it is so correlated with usual environmental changes that it helps an animal to find food, escape dangers, and produce offspring. By behaving in accordance with its hereditary pattern an animal usually continues to live. Considering the animal kingdom as a whole, behavior becomes more complex and nervous control becomes of increasing importance. The protozoa depend on cell responses; sponges have tissues which act as responding units; coelenterates have their behavioristic responses controlled to some extent by a rather loosely coordinated nerve net; worms show increasing domination of activities by polarized neurones which make up the ganglionic, segmental type of nervous system, which is so characteristic of annelids and reaches its climax in arthropods; the tubular central nervous system of chordates readily lends itself to the building up of controlling centers which produce general responses in particular types of organs, rather than in particular bodily segments (Parker, 1919). Yet in the most complex and highly coordinated of animals there are certain types of behavior which remain primitive. Even in man, where a specialized brain has made it possible for intelligence to serve as the finest

tool for making adaptive responses, there are activities which are largely or wholly controlled by rather primitive nerve nets or by glandular secretions and other chemical substances.

The activities of poikilotherms, and of a few homoiotherms, are limited by temperature and other factors in the environment and they may therefore be restricted to particular times of day or to particular seasons of the year. A hibernating animal is not wholly inactive. Certain of its physiological processes continue at a slow rate, but its behavioristic responses are absent. A poikilotherm therefore is not able to have continuous relations with environment by receiving sensory stimuli and responding in a more or less adaptive way through the activation of effectors. During enforced periods of quiescence it has a chance to forget lessons learned during previous experiences in its environment. Homoiotherms, with their separate pulmonary and systemic circulations and effective mechanisms for temperature regulation, permit their nervous systems to continue to function from day to day at a high level of activity. A homoiotherm, except for short periods of rest from fatigue, lives a continuously active life.

In general metabolism increases in rate with increased temperature, but every animal has an optimum range where it is most active and efficient and above which its activities may be abnormal. For example, an amoeba shows its maximum rate of locomotion at 21.5 deg. C. and above or below that temperature moves more slowly (Schwitalla, 1925). Ants crawl faster at higher temperatures (Andrews, 1927). Some animals are adjusted to high temperatures and some to low. In thermally stratified lakes and oceans particular species of fishes and plankton organisms are found regularly to

inhabit certain levels where the temperature range favors their metabolic activities. Some poikilothermic animals are very quick to perceive variations away from their optimum and quickly respond in such a way as to remain in favorable temperatures. This is true of herring (Powers, 1923), migrating salmon (Ward, 1921), various plankton animals (Pearse, 1926), animals in deserts (Buxton, 1923), and bats which live in caves (Hahn, 1908).

The behavior of many poikilotherms changes markedly with variations in temperature. A frog, for example, at temperatures above 10 deg. C. is usually strongly positive in its responses to light, but if the temperature falls below that, the frog becomes negative and if given an opportunity will burrow or crawl under some object, and at temperatures near 0 deg. C. becomes more or less torpid (Torelle, 1903). Sudden changes in temperature will cause a reversal of the usual responses of various animals to light (Mast, 1911). Such responses are usually adaptive. Among organisms which are negative to light at low temperatures Washburn (1926) mentions swarm spores, certain protozoa, an amphipod, and certain aquatic insects; among those which are positive at lower temperatures, certain copepods and annelid larvae. When planarians are subjected to increasing temperatures, between 23 and 26 deg. C. they become quite active and are positive to light; between 26 and 38 deg. C. they continue to crawl actively but become negative to light; and at 38 to 39 deg. C. the crawling becomes extremely active and is accompanied by violent twisting and turnings. Perhaps the sensations experienced are increasingly unpleasant.

A homoiotherm which is insulated with feathers or hair to prevent the loss of heat and has mechanisms to

check overheating can live a continuously active life with its body at the optimum temperature for metabolism. When the environment varies it may experience sensations of pain or discomfort to a greater degree than is possible among poikilotherms, but such suffering is the penalty for living continuously with full perception of stimuli. It is perhaps more than compensated for by the opportunity for mental development that continual living gives. Because they are able to live continually at an optimum rate birds and mammals are quicker, better coordinated, and more astute than reptiles, amphibians, or fishes.

A poikilotherm must seek an environment where a constant temperature obtains or confine its activities to favorable times. A constant environment is the ideal. A homoiotherm can not only remain active at all times but is able also to enjoy the intellectual luxury of seeking thermal variation in its environment. It thus gains a greater variety of experiences and these react to produce a more experienced and a more capable controlling nervous mechanism. The behavior of a homoiotherm therefore proceeds on a higher level than that of a slowly-responding, fitfully-living poikilotherm.

A few colonial insects have attained to the advantages which go with continuous living at temperatures approaching their optima. Honey bees gather in a close cluster, within a hive or hollow tree where they are protected somewhat from cold by wood insulation and there maintain a comparatively high temperature by metabolic activity. When their nest cavity cools, they beat their wings and raise the temperature, largely through muscular activity. The temperature of a cluster inside a hive may remain as high as 20 to 30 deg. C., while the temperatures outside are varying between 9 and 11 deg. C.

(Gates, 1914). Ant societies are not so well organized for maintaining high temperatures but some species build their mounds in such a way that they receive a maximum amount of energy from the sun. Tight roofs and inclosed air spaces help to maintain higher temperatures at night. Ants carry their eggs and young to the galleries within their nests where temperatures are most favorable. During prolonged cloudy and cool weather, however, they must remain quite inactive (Andrews, 1927).

As an individual, no poikilotherm is able to maintain a high, constant temperature in a varying environment. Homoiotherms, while attaining the ability to live continuously at a high rate, also gained the capacity to experience more varied sensations and to develop a better and higher degree of nervous control, consciousness, and intellect. Adaptation to life in variable land habitats has, through the development of a constant optimum bodily temperature, made intellectual life possible. The intellect gives endless opportunity for experiencing, remembering, foreseeing, planning, and surviving. It also allows the highest types of intellectuals to have leisure which is not spent altogether in thinking about surviving, but gives time for practice, amusement, and thought concerning better expedients for living, better ways of performing conventional social activities, the improvement of culture, and the extension of knowledge.

CHAPTER XII

FITNESS OF TEMPERATURE CONSTANCY

In his "Leçons sur les phénomènes de la vie" Claude Bernard concluded that "all the vital mechanisms, varied as they are, have only one object, that of preserving constant the condition of life in the internal environment," the blood—a very sagacious statement which has received much support from recent investigations. The evolution of the higher forms of life has been accompanied by a gradually increasing independence of environment. This has been achieved by the creation and maintenance within the bodies of such animals of a suitable environment for their constituent cells. The means by which animals have reached this state of independence is through increase in the cooperative functioning of their diverse tissues. This evolution has passed through four significant stages, which received their impetus from two evolutionary events—migration from salt water to fresh water and migration from water to land.

A properly balanced nutrient level was early established in the Metazoa about their body cells. By means of this the higher Metazoa acquired a considerable degree of independence in relation to fluctuations in their supply of nutrients. The sea offers a considerable degree of stability as an animal habitat. This is especially true in respect to its food resources. A nutrient level or reserve was not as essential for the maintenance of an

individual marine animal as for that of one on land, where the environmental conditions varied so greatly. That terrestrial animals have achieved the ability to maintain a rather uniform nutrient level is exemplified in the constancy of the composition of their blood, even in extreme environmental fluctuations. The blood of the higher forms has become of constant reaction. Thus fluctuations in the hydrogen-ion concentration of the environment do not noticeably affect that of the pericellular media. This is accomplished by the presence of "buffers" in the blood and the coordinated activity of the respiratory center and the kidney.

The more complex animals have also attained a resistance to, or independence of, variations in the salinity and osmotic pressure in the environment. In the sea, with its uniformity of salt content, there was little need for independence. The lower Metazoa contain almost exactly the same proportion and concentration of salts as the sea water which they inhabit. In the higher Metazoa the salinity and osmotic pressure of the blood may differ greatly from that of the surrounding medium. Internal constancy is maintained by the selective elimination of certain constituents by the kidneys. Macallum (1904) maintained that the saline composition of the blood of higher vertebrates closely resembles the probable composition of sea water at the time when the protovertebrate types first acquired a kidney. The latest stage through which certain animals have passed in becoming independent of environmental fluctuations through the attainment of a constant internal environment has been the maintenance of constant body temperature. In aquatic habitats, especially in the sea, the variations in temperatures are slight as compared to those in the air. Furthermore the range of variation in water is usually

within that tolerated by protoplasm, but the temperature of the air may vary much beyond such limits. Homoiothermism has been attained by the cooperation of nervous, metabolic, and vascular activities. Through it optimum conditions are ensured for the processes that must go on for the maintenance of the individual.

Homoiothermism apparently had its origin at the time when the great dinosaurs were becoming extinct and the newer but wiser mammals were rising. Variable climates were associated with, and perhaps stimulated, the development of a more precisely regulated internal temperature. The aridity of the earth at the end of the Paleozoic had its influence upon the terrestrial types, especially upon the more progressive of them. The strife between various types for food and water likely led to a more intensified living—a higher rate of metabolism—which implied a higher and more stable temperature. Then with increasing cold a premium was put upon such animals as could maintain their activity beyond the limits of the shortening summers. This was accomplished by the development of a mechanism whereby a relatively constant temperature could be maintained within the organism regardless of external conditions.

Thus it appears that the evolution of the bird and mammal, particularly the latter, was permitted by the concurrence of two factors—aridity and cold. Homoiothermism was not suddenly attained. It was a relatively slow process, just as was the emergence from aquatic habitats. Indications of imperfectly adjusted mechanisms are still to be seen in existing animals. An investigation of a comparative nature was conducted by Martin (1903), who states that Echidna is the lowest in the scale of warm-blooded animals. The attempt of this animal to attain homoiotherism fails to the extent of 10 deg. C.

when the environment varies from 5 to 35 deg. C. During cold weather Echidna abandons all attempts at homoiothermism and hibernates for four months with practically no difference between its body temperature and that of the surroundings. At high temperatures Echidna does not increase the number or depth of its respirations. It possesses no sweat glands and exhibits no evidence of ability to vary loss of heat by vaso-motor adjustment in response to changes in external temperatures.

Ornithorhynchus, which is also a primitive homoiotherm, is distinctly above Echidna, for, although its body temperature is low, it is fairly constant. This animal possesses numerous sweat glands upon the soft snout and frill but has none elsewhere on the body. Martin found that carbon dioxide production varied with the external temperature and this indicates that the animal can modify heat-loss as well as heat-production. Ornithorhynchus does not increase the rate of its respirations at high temperatures. Marsupials, however, show evidence of utilizing variation in heat-loss to a greater extent than it does, but less than higher mammals. Their respiratory rates are sometimes slightly increased at high temperatures.

Variation in production of heat is the ancestral method of regulating body temperature. Through developing a mechanism by means of which an organism may vary the production of heat in accordance with heat lost, animals have overcome the one great disadvantage of cold-bloodedness—activity is no longer dependent upon external temperature. At this stage a homoiotherm has also increased its ability to remain active at low temperatures. Later, by developing a mechanism controlling loss of heat, it increases its range in the direction

of high temperatures. Thus the higher mammal maintains its body temperature without direct reference to muscular activity, and metabolism may always proceed under optimum conditions.

In homoiotherms is seen the culmination of changes which began in the early communal life of Metazoa for the apparent advantage to be obtained from a relative independence from a fluctuating environment. Perhaps the word "advantage" implies a teleological explanation, but another view is equally plausible—that, through the agency of selection, evolution has been directed along the lines of modifications in the internal physiological environment of the organism as much as in morphological changes. Animals apparently become more specialized, or morphologically adapted, to particular environments when conditions are most stable. When conditions lack stability or are rapidly changing, evolution of morphological characters acquires no momentum. On the other hand the variations which lead to successive liberations from the influences of a varying environment would be of the greatest survival value in the environment of greatest instability. Such variations have proceeded along several lines, one of which has terminated in regulation at a constant temperature level.

For the organism as a whole the most favorable temperature is that which is conducive to the harmonious interaction of all its manifold activities. The attainment of a constant temperature by the homoiotherms has given them two advantages. (1) A temperature which is usually above that of the environment in which an animal lives permits a greater expenditure of energy. The velocities of chemical reactions going on in an animal's body are proportional to the ratio existing between the chemical force and the chemical resistance.

Chemical force is a function of free energy. Rise in temperature greatly diminishes chemical resistance. Temperature, therefore, is a very important factor in determining the velocity of reactions going on in a living organism. The homoiotherms manifest a rapidity of adjustment to external conditions which is far above that shown by the poikilotherms. In addition to the effects of a higher temperature on chemical reactions there is also an advantage on physical processes as in the diminution of the internal friction of liquids such as the blood, the hastening of diffusion, and the increasing of the velocity of conduction of nerve impulses. The influence of temperature on general metabolism has already been discussed. (2) A constant temperature level, which assures the organism that its physiological processes shall continue in a state of equilibrium, which is optimum for the processes involved, is the second advantage. A constant internal temperature thus protects the organism against environmental irregularity.

It is common knowledge that in homoiotherms physiological processes take place most readily at body temperature. The value of a constant temperature level is readily seen in the case of enzymotic activity. The enzymes are effective only through a very well defined range of temperatures. Moreover, their maximum rate of reaction takes place at optimum temperatures which are very near those of the bodies of homoiotherms. While many chemical reactions show acceleration with increased temperature, enzymes do not absolutely follow this rule. They increase their activity from 0 deg. C. to about 40 deg. C., but beyond that show a gradual decrease. At 60 deg. C. enzymes are destroyed. The enzymes of the poikilotherms have optima like those of homoiotherms. Early workers regarded the optimum as a mystery and

it was used as an indication of "vitalism." It is now known that with enzyme action, as with certain other chemical reactions, a rise in temperature quickens catalysis, in accordance with the temperature coefficient of chemical processes generally, but also renders an enzyme less stable, so that it breaks down more and more rapidly as the temperature rises. The temperature at which the maximum rate is shown is therefore that at which the acceleration due to temperature is in greatest excess over the simultaneous destruction of the enzyme, and is known as the optimum. Thus the fitness of the constant temperature level of homoiotherms can be readily appreciated.

Heat is not to be regarded as the cause of body processes; it is only one of the conditions. The extent to which heat may influence such processes is relative and varies with the quantity available in kinetic form. The constancy of temperature maintained at the particular level represented in the homoiotherms permits the continuity of the physiological processes of animals at their maximum effectiveness, independent of environmental caprice—and therein lies its fitness!

CHAPTER XIII

MAN AS A HOMOIOTHERMIC ANIMAL

Man is a mammal and shows greater similarities to anthropoids and other primates than those animals do to other orders of mammals. On the other hand, he shows certain rather striking differences from other primates, but these are largely in degree rather than in kind. His growth in length takes place at a fairly constant time rate when his increase in weight takes place at a constant percentage rate. This indicates that "the physiological environment with respect to growth-limiting process remains constant" (Brody, 1928). The blood of man is the fluid medium which bathes active living cells, and is remarkably constant in its composition. It contains buffers, rather definite proportions of nutrients and wastes, and various mechanisms for maintaining uniformity. By adding or removing insulation in the form of clothing and by frequenting dwellings man is able during most of his life to live in conditions which are uniform and on the whole conducive to his physiological and mental efficiency, and to his peace of mind.

Stability.—In all habitats and among all groups of the animal kingdom animals seek stability. An animal has better chances of surviving if the environment in which it lives is dependable. Some animals attain this end by living in an environment which is unvarying. Others live in variable environments and vary with them.

Homoiotherms as a whole have become more or less independent of environment by attaining the ability to maintain a constant and comparatively high body temperature. Man, more than any other animal, is able to live to his full capacity at all times. For this privilege the constancy of the environment of his cells, tissues, organs, and body is largely responsible.

It is "human nature" to long for stability. A man believes that if he could cease to worry about making a living and surviving, living better than his fellows (or being a success), his state after his present life, and other vexatious matters, he would be perfectly happy and contented. But would he? There is a certain satisfaction in overcoming difficulties and in enduring hardships. An easy, contented, assured existence must be monotonous. Is continual struggle better than monotony?

Climate.—Climate is a potent factor in limiting or enforcing natural abilities. In regions where conditions of life are severe men may expend most of their energies in living, but where there is an abundance of food and an easy life is possible, culture may reach a high level of development. Probably the most important climatic factors which influence the attainments of human socities are temperature, humidity, and wind (Barbour, 1921). On the wind-swept arctic barrens there are no great cities, no universities or factories. The same is true of the Sahara Desert and of the Amazon Basin. The human race is not at its best where the climate is monotonous. It makes no difference whether the monotony is cold and bleak, hot and dry, or hot and wet.

Caucasians and perhaps other races are at their best in the temperate regions. Frequent changes in temperature, humidity, and wind appear to have a tonic effect

on the human race and man does his best work where such variations obtain (Huntington, 1915). Thus, though man strives in general to make his physiologic, psychic, and economic conditions for living as uniform and dependable as possible, he does not reach his greatest degree of accomplishment in monotony.

Frigid and Tropical Regions.—The frigid regions of the earth produce little on land, but the sea has long been exploited for its food resources. The tropics have not been the seat of much human achievement. There are perhaps several reasons for this, but two are noteworthy: (1) hot, monotonous climate and (2) disease. The humid tropics, though often producing an abundance of plant and animal life, have never been the environment for the highest types of civilization. The characteristic racial stocks in tropical countries are Negroids, Malays, Mongolians, and Semitics. With the clearing up of tropical diseases, Caucasians are dominating tropical countries more and more, but Caucasians as a rule do not flourish in the tropics. Perhaps it will be best for the world to leave the tropics as the home of comparatively primitive, simple people who will work for low wages and furnish raw materials for the more aggressive and progressive peoples in temperate zones. There is no question but that the dark-skinned races are more healthful than Caucasians in warm countries.

There are certainly racial peculiarities which make some types of men better adapted to certain climates than others. White men who go from temperate to tropical countries show reduced basal metabolism (Knipping, 1925; Fleming, 1925). Native inhabitants of the tropics have a lower blood pressure than people who have recently come from temperate regions (Cadbury, 1923). There are fundamental differences in metabolism be-

tween blacks and whites (Woodruff, 1916). In comparable areas of skin the former have more sweat glands than the latter. The basal metabolism of the white natives in tropical Brazil was found by Almeida (1919, 1920) to be 24 per cent lower than in the inhabitants of temperate zones. "Their habitual intensity of heat production is a factor additional to the law (Rubner-Rictet) of surface area, and its lowering is regarded as an adaptation to their environment, and an advantage in their struggle against high air temperatures." The same holds true for the colored inhabitants of Brazil. On the other hand Eijkman (1921) found in the Dutch East Indies that the basal metabolism of blacks and whites was about the same as of those in temperate climates. In reviewing these papers Halliburton notes that white men in warm dry climates usually have a high color and profit by exercise, while those in warm moist climates are often pale and take little exercise. There is need for more knowledge concerning the effects of tropical climates on the various races of men.

Life Indoors.—As civilization progresses man has less contact with pioneer conditions of life; his environment and his daily, annual, and perennial life become more and more monotonous. He must therefore take thought for the morrow and, while insuring stability in his living, also retain the variety which is the spice and leaven of life. A dwelling should not furnish such an artificial environment that it is monotonous or abnormal. Colds are incubated in steam-heated houses where there is insufficient moisture. Tuberculosis flourishes among those who live indoors in dust and darkness. The great mass of the Chinese people is docile, unprogressive, hopeless, and stolid largely on account of monotony—sameness in diet, social contacts, and outlook for the future. Man

must attain stability, but, equally, he must avoid monotony.

Conclusions.—Man today proudly dominates the earth. He has attained to his present position through a long struggle up from ancestors in the dim past. Gill-breathers in the water attained some ability to live on land, developed lungs, and took up terrestrial life. At first land vertebrates lacked proper insulation. Doubtless many of them lost the water from their bodies and died. But as time went on tough skins developed which held water in. Later these skins grew specialized feathers and hairs which served to conserve bodily heat as well as water. Then constant temperatures at optimum levels for metabolism became possible and were developed through various controlling mechanisms. Given a constant bodily temperature, which permitted perennial activity, and a highly efficient brain, man has been able to excel all competitors by inventions which make him more independent of environment than any other animal. Yet, he is not, and probably never will be, wholly emancipated. He must still be more or less "natural."

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